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ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

Should internet sites be mentioned in the bibliographies of scientific publications?

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In the 19th century, when a long-gone optimistic attitude towards the future of our civilization was prevailing, science was seen as a permanent process of increase of our positive, rational knowledge, not only in the aim of being able to act more efficiently, i.e. to improve our technical mastership, but also in the hope of getting a more comprehensive basic understanding of all aspects of the world we live in, by pure intellectual curiosity. At that time, it was considered of utmost importance to maintain a permanent link between all historical periods of development of science: any new finding, any new theory, was placed in this historical context and was viewed as the addition of a new stone to an edifice to the building of which all scientists of the past had contributed. Times have changed, and many scientists have now adopted a much more limited scope in their activity, either by being only interested in the development of scientific knowledge having predictable, and often immediate, practical applications, or by feeling only concerned with recent findings and theories, without including them in a more general apprehension of the evolution of scientific knowledge. The fact that, quite recently, a paper using (in a specific context, that of zoological nomenclature) a formula like "tyranny of the past" to qualify this permanent link between current and previous science, has been accepted for publication by different scientific journals (SAVAGE, 1990*a-b*, 1991), is an interesting illustration of this trend.

The laboratory in the Paris Museum where I have been working for thirty years is on the other side of a street bordered by two major French Universities, and in the last decades I have not unfrequently found, in the dustbins of the latter, piles of journals, especially those, like *Nature* or *Science*, which, being published weekly, represent a large volume of paper each year: questioned about this researchers or librarians of these Universities would reply that their laboratories or libraries are too small and lack space to store important amounts of scientific literature, and that furthermore, after a certain time has elapsed, these publications have become "obsolete" and are no more "useful" for ongoing research: for this latter reason, they did not even think useful to query, before throwing these publications away, if other scientific laboratories or libraries would be interested in recovering them. Clearly, for a number of scientists nowadays, scientific publications have become a short-term-use product, like many other products in our society. That this attitude has strong influences on the course of scientific research itself is hardly to be demonstrated: never before has scientific research more slavishly followed fashions, with some dominant ideas, techniques, methods or research subjects being supported or explored by many researchers and teams during a decade or two, and then completely abandoned when other more recent ideas or subjects supplant them in the fund-raising systems of science, and, by way of consequence, in the minds of many.

Such a way of functioning of science may be very efficient whenever science is viewed merely as a way to produce more efficient or cheaper pharmaceuticals, pesticides, cosmetics, computers, cars, satellites or weapons, i.e. as a basic support to technical improvement, but it may not be so if science is also understood as aimed at a better understanding of the world we live in, irrespective of any aim at acting upon it or at modifying it. If science is to be a progressive construction of a complex corpus of knowledge, i.e. of facts and theories about these facts, it is highly questionable

whether any scientific publication ever becomes "obsolete": it is part of a complex edifice, and suppressing or ignoring it may be like removing a stone at the basis of a wall. Stating that current science can be understood and mastered without connection with the past of science is similar to saying that the architecture, painting, music or literature of the past are now "obsolete" and should be forgotten or destroyed to replace them by the works of our time.

In some scientific fields, the progress of research is so quick, and the competition between researchers, research teams or even countries so strong, that many new results or theories, at the time when they are published, are already "obsolete", in the sense that they are already known of several other researchers and teams. In such research fields, it is striking that the bibliography of a paper often contains many references to works quoted as "personal communication", "unpublished data", "work in progress", "in preparation" or "in press". Of course, this may cause problems later if subsequent authors wish to trace these "phantom publications", which not rarely happen not to have ever been actually published after having been quoted (see DUBOIS, 1999): hence the recommendation, which is even an editorial rule in some periodicals, not to mention such "references" in a bibliography. The same problem applies to the growing practice consisting in quoting internet sites as bibliographic references in scientific papers or books. In fact, such references are of the same nature as a "personal communication": in the future, they won't be available to readers of the publication where they are quoted. An internet site has no permanency, as it can be modified, "updated", "corrected" or suppressed at any moment. No long-term trace is usually kept of what was available on a site at a given date, and even if such a memory is kept privately by the owner or editor of a site, it is not directly available to customers.

The function of a list of "references cited" at the end of a scientific paper is double: (1) to provide the sources of information used by an author to support some of the scientific statements contained in the paper as valid or discussed in the paper; (2) to allow any reader of the paper to go back personally to these sources and to study them exactly as they were when they were quoted. In order for a bibliography to be useful, all references that appear there should be accessible to any reader, and should remain so in the future, whatever the fate of the authors of the works or of the paper where these references appear. This condition does not apply to works quoted as "personal communication" or "in press" (except if the precise reference of the future publication can be provided with certainty), and similarly does not apply to internet sites. The problem here does not come from internet sites being on a support other than paper, but on their having no permanency. Some non-paper publication systems, such as CD-Roms, audio or video cassettes, can be as permanent and non-modifiable as paper publications, and qualify for "publications" that can be quoted in a bibliography: for this reason, such works can be considered as publications for the purposes of the *International Code of zoological Nomenclature* (ANONYMOUS, 1999), which is not the case of internet sites.

No one knows what will be the long-term fate of our society, of the activity we call science and of the corpus of results and theories produced by this activity. However, as soon as a scientific periodical places itself within the frame of long-term science, "as if science was still to exist for many decades and centuries", it should care for publishing only bibliographic information that will be available for readers in the long-term future. For this reason, the periodical *Alytes* does not accept the mention of internet sites among the references listed in the *Literature cited* section of a paper. If absolutely necessary for the understanding of the text, or to provide some information that would not be available otherwise, exceptional mention of an internet site in the corpus of the text may be acceptable, just like in some cases it is acceptable to mention a "personal communication" or "unpublished data". But this reference won't be repeated in the bibliography. In most cases, information that may *today* be easier to find on an internet site may also be available in paper-published works: although it may be a little more time-consuming for an author to trace such a published information, mention of such a published reference will, in the long run, be much more useful to the future readers of the paper and is worth the effort to find it.

For the same reason, i.e. the need of a long-term accessibility of all the information mentioned in the papers it publishes, the journal *Alytes* does not put a priori limitations on the length of papers or of tables of data and results of scientific works submitted to the journal: "*Alytes* encourages the publication of complete tables of original data, that can be used by subsequent authors for further analysis or critical reevaluation, rather than simply providing results of statistical tests, phylogenetic analyses, etc." (DUBOIS, 1997: 188). This also means that *Alytes* does not encourage authors to state that additional detailed data are available at their address and can be obtained by writing directly to them, or are available online (e.g., as "supporting online material"): what will be the fate of such pieces of information in 50 or 100 years? Either this information is useful for the understanding of the paper and evaluation of its merits, and then it should be included in the paper (even as a long table or appendix), or it is not, and then it should not be mentioned at all.

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Orientation and migration distances of a pond-breeding salamander (*Notophthalmus perstriatus*, Salamandridae)

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Habitat loss and modification have played a significant role in the decline of amphibian populations and species. Loss of wetlands, which are used as breeding sites for many amphibians, has contributed to the decline. The protection of small, isolated wetlands and core areas of associated uplands is one way in which population declines in certain species can be slowed or prevented. Nevertheless, migration distances of individuals of most amphibian species from their breeding sites are unknown. Using drift fences and pitfall traps, I studied migration distance and orientation of striped newts (*Notophthalmus perstriatus*) at a breeding pond in northern Florida, USA. Newts entered (immigration) and exited (emigration) the pond basin in a nonrandom fashion but no obvious effects of upland habitat were apparent. Patterns of emigration and immigration differed significantly between sexes, life-history stages, and migration events. Individuals tended to exit and enter the pond basin within the same quadrant, sometimes leaving and returning at the same point. Newts moved hundreds of meters into the sandhill uplands surrounding the pond. I found an inverse relationship between the proportion of newts migrating and distance from the pond. Nonetheless, I estimated that at least 16 % of individuals breeding at the pond migrated in excess of 500 m from the pond. Thus, a core of protected upland with a radius of approximately 800 m from the pond would be needed to preserve the area used by the vast majority of individuals that breed at the pond. These data underscore the need to study upland habitat requirements for amphibians; findings for one taxon (e.g. *ambystomatids*) may not be applicable to others (e.g., salamandrids). Without such data, designating terrestrial core habitat to conserve aquatic-breeding amphibians will be difficult or impossible. However, without better protection of small, isolated wetlands, arguments to preserve surrounding uplands are irrelevant.

INTRODUCTION

During the past two decades, amphibian declines have received considerable attention (BARINAGA, 1990; WAKE et al., 1991; WAKE, 1991; ALFORD & RICHARDS, 1999; HOULAHAN et

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al., 2000). Although pathogens have been implicated in several die-off events (BERGER et al., 1998; LIPS, 1998, 1999), there is a consensus among herpetologists that the global decline is a result of multiple factors (ALFORD & RICHARDS, 1999). Habitat modification and destruction have been identified as significant factors contributing to the global decline (DODD, 1997; ALFORD & RICHARDS, 1999; DUELLMAN, 1999; SEMLITSCH, 2000). Although they do not attract the media attention that mass mortality or deformed amphibians receive, habitat modification and loss are insidious processes that must be addressed if amphibians are to persist. The effects of habitat changes on amphibian populations are of particular concern in areas that are characterized by a high density of small, isolated wetlands (DELIS et al., 1996; HECNAR & M'CLOSKEY, 1996; KNUTSON et al., 1999; BABBITT & TANNER, 2000; SEMLITSCH, 2000; SNODGRASS et al., 2000; RUSSELL et al., 2002). In these areas (e.g., the Southeastern Coastal Plain of North America), amphibian diversity is high (DUELLMAN & SWEET, 1999) and many species rely solely on small, isolated wetlands as breeding sites (DODD, 1997; SEMLITSCH & BODIE, 1998; BABBITT & TANNER, 2000).

Despite their size (i.e., less than a few hectares), small, isolated wetlands are of tremendous biological importance, particularly for amphibians. They play a vital role in amphibian metapopulation dynamics and therefore are essential in maintaining viable populations of amphibians at a landscape scale (SEMLITSCH & BODIE, 1998; SEMLITSCH, 2000; SNODGRASS et al., 2000). In addition to amphibians, numerous other vertebrates and a suite of invertebrate species depend on small, isolated wetlands (BROWN et al., 1990; MOLER & FRANZ, 1988; BURKE & GIBBONS, 1995; HART & NEWMAN, 1995; SEMLITSCH & BODIE, 1998; RUSSELL et al., 2002).

Preserving a wetland alone may not result in protection of many of the organisms that depend upon the wetland. Many amphibians have complex life cycles in which they require ponds to breed but spend the majority of their lives in surrounding upland habitats (DODD, 1997; DODD & CADE, 1998; SEMLITSCH, 1998; SEMLITSCH & JENSEN, 2001). If sufficient upland habitat surrounding isolated breeding-ponds is not preserved, amphibians with complex life cycles are not likely to persist at a local scale. Therefore, at some point the loss of uplands may lead to extirpation of some amphibian populations because of disruption of metapopulation dynamics (SEMLITSCH & BODIE, 1998; SEMLITSCH, 2000; MARSH & TRENHAM, 2001), even when the ponds themselves are preserved.

One strategy to curtail the loss of amphibians associated with habitat alteration around small, isolated wetlands is to preserve "core habitat" and "buffer zones" consisting of protected uplands surrounding the wetlands (SEMLITSCH & JENSEN, 2001). These zones provide habitat for retreats and foraging for those species with complex life cycles, many of which are now considered common. Without preservation of appropriate upland habitat, even common species will decline.

Little is known, however, about the extent of upland "core habitat" required by pond-breeding amphibians. DODD (1996) summarized the literature on upland movements of amphibians in North America and found that this distances amphibians migrate from breeding sites are poorly known. From this summary and a review by SEMLITSCH (1998) on migration distances of ambystomatid salamanders, it is apparent that many amphibians move considerable distances from breeding ponds. Unfortunately, migration distances are only available for a few species and usually are based on a single or a few individuals. Clearly there

is need for data on migration distances from breeding sites for most North American amphibians. These data are essential to justify establishing adequate "core habitat" of uplands around amphibian breeding ponds.

I collected data on orientation and migration distances for striped newts (*Notophthalmus perstriatus*) at a breeding pond and in the surrounding uplands in north-central Florida. Striped newts breed exclusively in small, isolated wetlands that lack fish. They have a complex life cycle and individuals spend much of their lives in uplands surrounding breeding ponds (CHRISTMAN & MEANS, 1992; DODD & LACLAIRE, 1995; JOHNSON, 2001, 2002; DODD et al., in press). Striped newts are restricted to xeric uplands (i.e., sandhill and scrub communities) and are endemic to southern Georgia and northern Florida, USA (fig. 1). The species has declined throughout its range (DODD & LACLAIRE, 1995; FRANZ & SMITH, 1999) and its biological status is under review by the US Fish and Wildlife Service (L. LaClaire, pers. comm.). The objectives of my study were (1) to determine orientation patterns of striped newts into and away from a breeding pond, and (2) to determine migration distances of individuals into the surrounding upland habitat.

MATERIALS AND METHODS

STUDY SITE

The study was conducted on the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam Co., Florida, USA (29°41'N, 82°00'W; fig. 1). EISENBERG & FRANZ (1995), LACLAIRE (1995) and DODD (1996) provided descriptions of the preserve and its habitats. Data were collected from 7 October 1996 to 11 September 1998 at One Shot Pond (OSP). OSP is a small, isolated pond with a variable hydroperiod (hydroperiod refers to the number of days a pond holds water between periods when it is dry) and is located in xeric sandhill uplands dominated by longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*) and wiregrass (*Aristida beyrichiana*). Small stands of planted slash pine (*Pinus elliottii*) are located north and southwest of the pond basin (fig. 2). Several water bodies are located near OSP (fig. 2). These water bodies are isolated from one another and only receive water from rainfall and ground water seepage; their hydroperiods are dictated by fluctuations in the water table. Fox Pond held water from 26 November 1997 until the end of the study, whereas OSP, Berry Pond, Lake McCloud and the Anderson Cue Lakes held water throughout the entire study period. During the study, striped newts were only present in OSP and Fox Pond. However, only 32 newts (16 adults and 16 juveniles) were captured at Fox Pond (S. A. Johnson, unpublished data). McCloud and the Anderson Cue lakes support predatory fishes, and striped newts do not breed there. No striped newts were captured during periodic sampling throughout the study period in Berry Pond. Because there were no other breeding ponds within several kilometers of OSP, I assumed that striped newts caught in upland fences around OSP originated from within OSP.
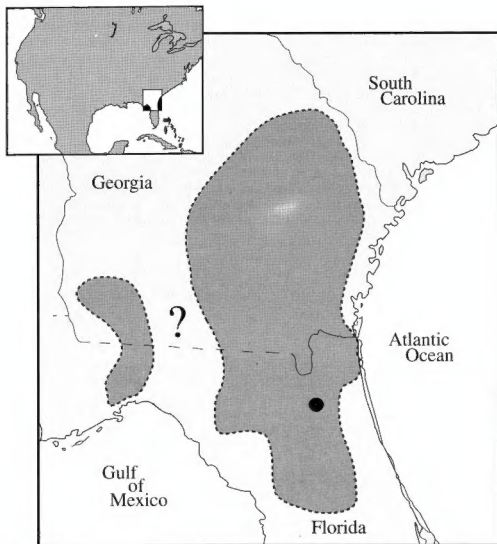
Fig. 1. – Geographic range of striped newts, which are endemic to Georgia and Florida, USA. Note the hiatus (?) between the western and eastern portions of the range. This area likely represents a true gap in the species distribution, rather than an artifact of inadequate survey effort. The black dot (•) shows the location of study area, Katharine Ordway Preserve, Putnam Co., north-central Florida, USA.

ORIENTATION AT ONE SHOT POND

I encircled OSP with a 190-m drift fence made of galvanized metal flashing that was buried ca. 15 cm below the ground, with ca. 35 cm extending above the ground. Thirty-eight pitfall traps (19-l plastic buckets) were buried flush with the ground. Pitfall traps were placed
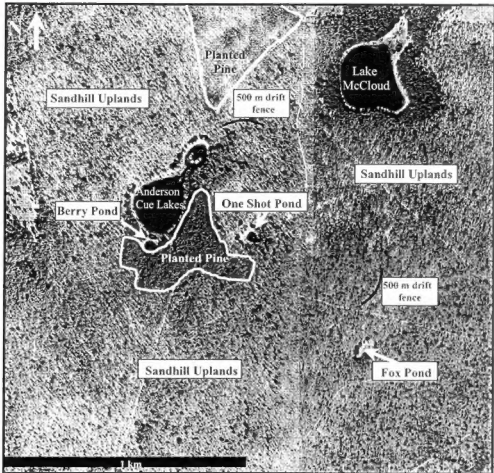
Fig. 2. – Aerial photograph of the study area in 1999. The predominant upland habitat type is xeric sandhill. The approximate locations of the 500 m drift fence sections (see fig. 3) are indicated. Dirt roads appear as thin, white lines.

in pairs, one on each side of the fence, at intervals of about 10 m. I usually checked traps three to five days per week, depending on weather and movements of animals. I weighed and measured newts caught in pitfall traps at the pond and in the surrounding uplands. Each newt was individually marked by toe clipping (DONNELLY et al., 1994) and released on the opposite side of the fence. Sex of adults was determined by the presence of a conspicuous whitish gland visible at the posterior edge of the vent in mature males. Recently transformed newts were recognized by the presence of gill vestiges visible for several days after metamorphosis. Recently transformed newts with swollen vents were presumed to be mature (JOHNSON, 2001), and aquatic sampling in the pond showed that such individuals represent paedomorphic

animals that recently bred. These newts are referred to as paedomorphs. Transformed newts without swollen vents (i.e., immatures) are referred to as efts.

I obtained a compass orientation for each pair of pitfall traps surrounding OSP. To do this, I stood in the center of the pond and took a bearing on each pair of traps at the drift fence. Following the methods of DODD & CADE (1998), I used Rao's spacing test (RAO, 1976; BATSCHELET, 1981) to determine if captures were distributed uniformly around the drift fence (i.e., random orientation). I analyzed orientation of newts into and away from the pond by sex and life history stage. I made comparisons between distinct migration events (JOHNSON, 2001) within the adult and eft life-history stages. For comparisons between sexes, life-history stages, and migration events, I ran the same multirespsonse permutation procedure (MRPP; MIELKE & BERRY, 2001) used by DODD & CADE (1998). Orientation analyses were performed with the statistical software package BLOSSOM, which was developed by the US Geological Survey (CADE & RICHARDS, 1999). BLOSSOM is available free at www.fort.usgs.gov/products/software/software.asp.

UPLAND MIGRATION

Migration distances of newts in the sandhill uplands around OSP were determined through captures in pitfall traps associated with drift fences. Drift fences were oriented to capture newts during movements to and from the pond (fig. 3). In year one, five fence sections were established at each of four distances from OSP (20 m, 40 m, 80 m and 160 m). Fence sections at each distance totaled 20 % of the circumference at that distance from the pond. Fence sections were distributed evenly at each distance, and they did not overlap with fence sections at the other distances (fig. 3a). Fence sections at 20 m were 10.0 m long with 4 pitfalls (2 on each side of the fence); at 40 m fence sections were 15.1 m with 6 pitfalls; at 80 m sections were 25.1 m with 8 pitfalls; at 160 m sections were 45.2 m with 10 pitfalls. Pitfall traps were installed on both sides of the upland fences (i.e., pond side and upland side; fig. 3a). This upland fence array was monitored from 7 October 1996 to 5 December 1997, and fences were constructed similarly to the fence at the pond.

Results from year one demonstrated that striped newts regularly moved more than 160 m. Therefore, a new upland fence array was installed in year two, with upland drift fences erected much farther away from OSP. On 5 December 1997, the upland drift fences described above were replaced with a different array of fence sections (fig. 3b) and the new fences were in place by 7 December 1997. These fences were constructed of heavy-gauge silt-fence material buried ca. 15 cm into the ground – ca. 40 cm extended above ground. Two fence sections were installed at each of five distances (100 m, 200 m, 300 m, 400 m and 500 m) from the pond. Fence sections at each distance totaled 13.4 % of the circumference at that distance from the pond, and fence sections overlapped (fig. 3b). The two fence sections at 100 m were each 42 m long with 6 pitfalls (3 on each side of the fence), installed evenly throughout each section; at 200 m sections were 84 m long with 10 pitfalls; at 300 m sections were 126 m long with 14 pitfalls; at 400 m sections were 168 m long with 18 pitfalls; at 500 m sections were 210 m long with 22 pitfalls. Pitfall traps were oriented in the same manner as year one; pond-side traps were on the side of the fences toward OSP and upland-side traps were away
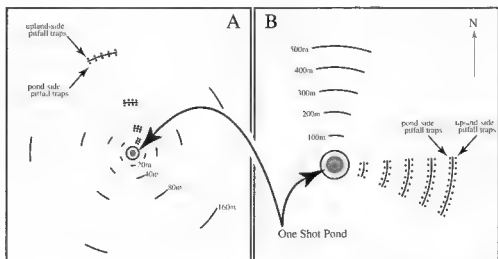
Fig. 3 Upland drift fence arrays around One Shot Pond, Putnam Co., Florida, USA. The upland array design in year one of the study is depicted in A and the year two design is depicted in B. One Shot Pond is shown as a solid circle, and the circle around it represents the drift fence at the pond.

from OSP (fig. 3b). The upland fence array in year two was monitored until the study ended on 11 September 1998.

In total, 280 pitfall traps were installed at upland fence sections and were monitored during the 2-year study, for a total of 98,140 trap-nights (one trap-night means one pitfall trap open for 24 hours). Upland traps were checked on the same schedule as those at the pond and newts were processed as described above.

Based on captures at upland fence sections and at the outside of the drift fence encircling OSP, I estimated the proportion of the newt population that migrated different distances from the pond. Data used in the estimates were confined to 7 December 1997 through 31 March 1998. During this period, there was a mass migration of newts toward the pond and very little movement away from the pond (JOHNSON, 2001). Ninety-one percent of upland fence captures during year two occurred during this period. These captures, however, only represented newts that migrated through a subset of the surrounding uplands. Because upland drift fences sampled only 13.4% of the uplands at each distance, I multiplied the number of captures in the outside pitfalls by 7.5. The product of this calculation is an estimate of the number of captures expected at each distance had the upland fence sections sampled 100% of the uplands at each distance. For each upland fence section, I divided the estimate by the number of total newt captures on the outside of the fence at OSP to approximate the proportion of individuals that had migrated various distances (i.e., 100 m to 500 m, at 100 m intervals). I assumed there was no strong nonrandom orientation of newts moving through the uplands. Nonetheless, movement of newts into and away from the pond was nonrandom (see below), but there was no overwhelmingly strong directionality that would violate this assumption

However, estimates of the proportion of newts that migrated various distances from the pond are probably conservative

I use the term "migration" to indicate seasonal, two-way movements of newts away from and toward a breeding pond. "Immigration" indicates a general pattern of migration toward the breeding pond, whereas "emigration" indicates migration away from the pond (SEMLITSCH & RYAN, 1999). "Dispersal" refers to "once-in-a-lifetime" movement away from a pond and infers that the dispersing individual will not return to its natal pond.

RESULTS

ORIENTATION AT ONE SHOT POND

All patterns of adult immigration and emigration were significantly nonrandom (fig 4; Rao's spacing tests, all $P < 0.001$). Adult striped newts entered and exited the pond in all directions. They tended to enter the pond basin primarily from the east and west (fig. 4). Adults emigrated in all directions but there was a single, distinct angle of emigration, as indicated by the relatively high number of captures in a pitfall trap located at a south-southeast direction (fig 4) Emigration of paedomorphs and efts also was nonrandom (fig 5; Rao's spacing tests, both $P < 0.001$). There was no obvious pattern to paedomorph emigration, but emigrating efts exited the pond basin most often in the southwest quadrant (fig. 5)

Overall patterns of immigration differed significantly from emigration for females and males (tab. 1) Although the directionality of immigrating adults appeared similar between the sexes (fig. 4), patterns were significantly different (MRPP test, $P = 0.002$). There were three distinct immigration events of adults, but orientation patterns were significantly different between the sexes only during the third, and largest of these events (tab. 2). Differences in emigration between males and females (fig 4) were not significant overall or when distinct emigration events were compared (tab. 1-2).

There were two distinct emigration events of recently transformed striped newts comprising the 1996-97 cohort. The first emigration event took place from October through November 1996, and the second event from April through June 1997 (JOHNSON, 2002). Immature newts (i e , efts) comprised the first event, whereas emigration later consisted mostly of recently transformed paedomorphs (JOHNSON, 2002) Patterns of emigration were significantly different between the eft and paedomorph life-history stages of the same cohort (tab. 1). In addition to the eft emigration of 1996, a second emigration event of efts took place from June through early September 1998 (JOHNSON, 2002). Patterns of eft captures at OSP differed significantly between these two emigration events and, considering all efts and all adults, efts exited the pond basin in a different pattern from adults (tab 1-2).

Data for 44 individually marked efts initially caught leaving the pond in the winter of 1996 and recaptured when they returned to breed in the winter of 1997 indicated that individuals tended to enter and exit the pond within the same quadrant. Sixty-four percent of these newts left and returned to OSP in the same quadrant, and four individuals (9 ") were caught leaving and returning to the pond at the same pair of pitfall traps. The vast majority of
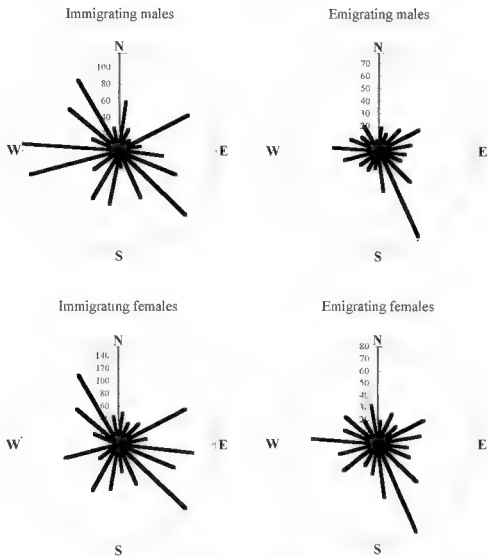
Fig 4 Orientation patterns of immigrating and emigrating striped newt adults captured in pitfall traps at a drift fence encircling One Shot Pond, Putnam Co., Florida, USA. Orientation was significantly different from random for all four patterns. The length of the lines indicates the number of newts entering and exiting the pond basin at each pitfall trap
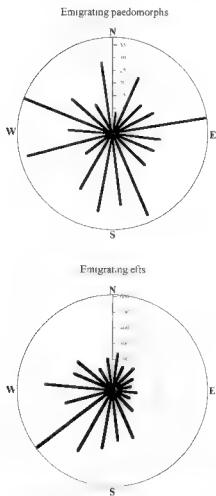
Emigrating paedomorphs

Emigrating efts

Fig 5   Orientation patterns of emigrating striped newt paedomorphs and efts captured in pitfall traps
at a drift fence encircling One Shot Pond, Putnam, Co., Florida, USA. Orientation was significantly
different from random for both patterns. The length of the lines indicates the number of newts
exiting the pond basin at each pitfall trap.

Table 1.   Overall comparisons of directional orientation patterns for striped newts entering (immigrating) and leaving (emigrating) One Shot Pond, Putnam Co., Florida, USA

Comparison	n	Standardized test statistic	P
Immigrating vs. emigrating males	1159, 486	− 13.317	< 0.001
Immigrating vs. emigrating females	1489, 645	− 3.798	0.008
Immigrating males vs. females	1159, 1489	− 5.524	0.002
Emigrating males vs. females	486, 645	− 0.437	0.2
Emigrating efts vs. emigrating adults	5008, 1131	− 67.639	< 0.001
Emigrating efts vs. emigrating paedomorphs of the same cohort	745, 407	− 9.506	< 0.001

Table 2.   Comparisons of directional orientation patterns for striped newts entering (immigrating) and leaving (emigrating) One Shot Pond, Putnam Co., Florida, USA

Comparison	n	Standardized test statistic	P
Immigrating males vs. immigrating females	*	*	*
− Immigration Event 1	23, 13	0.697	0.7
− Immigration Event 2	22, 66	− 0.130	0.3
− Immigration Event 3	1049, 1290	− 4.008	0.006
Emigrating males vs. emigrating females	*	*	*
− Emigration Event 2	15, 68	0.686	0.7
− Emigration Event 3	430, 484	− 0.005	0.3
Emigrating efts during metamorphic Event 1 vs. emigrating efts during metamorphic Event 3	745, 4237	− 3.599	0.01

individuals (84 %) entered the pond basin within the same half they had exited from the previous year.

MIGRATION INTO UPLANDS

I captured 831 newts in the upland drift fences during year one (fig. 3a, tab. 3). Pond-side captures accounted for 73 % of total captures, and migration in year one consisted primarily of recently transformed efts that were moving into the uplands. I captured newts at all of the upland fence sections (fig. 3a, tab. 3) and in most (91.4 %) of the pond-side pitfall traps.

Table 3 – Numbers of striped newts captured in pitfall traps at drift fence arrays in the sandhill uplands surrounding One Shot Pond, Putnam, Co., Florida, USA. Drift fences were located at various distances from the pond. See fig. 3 for a depiction of the arrays.

	Year 1				Year 2				
	20 m	40 m	80 m	160 m	100 m	200 m	300 m	400 m	500 m
Pond-side	140	126	169	172	11	6	10	12	7
Upland-side	79	39	64	42	121	108	86	86	48
Total	219	165	233	214	132	114	96	98	55

During each period of migration most newts were captured on the same sides of upland drift fences. However, for some movement events, a few newts were captured in pitfalls on the opposite side of fences from the majority of captures. I believe this is because there was a small degree of wandering by some newts in the uplands as they moved to or from OSP. Pond-side captures at upland fences in year one represented three distinct periods of newt migration, two emigration events and one immigration event (tab. 4). Most newts captured on the pond-side of upland fences in year one (76 % of pond-side captures) were caught during the first emigration event (i.e., E1), which occurred from October 1996 through February 1997 (tab. 4). Emigration during this period consisted almost exclusively of immature efts that had recently transformed. I captured far fewer newts (15 % of pond-side captures) during emigration event two (E2), which occurred from April through July of 1997 (tab. 4). This emigration event was comprised of recently transformed paedomorphic newts (54 % of the migrating newts), as well as recently transformed efts and several adults that likely had finished breeding and were moving back into the uplands. The third period of migration, indicated by pond-side fence captures in year one, was the result of an immigration event (i.e., I3) that began in October 1997 (tab. 4). There was a major breeding migration of adults into the pond that began in October 1997 and pond-side captures at this time probably resulted from adults that were moving toward the pond but happened to be captured on the pond-side of the upland drift fences (tab. 4).

Upland-side captures of striped newts accounted for 27 % of captures in year one. I captured newts at each of the five fence sections (fig. 3a), at each distance from OSP (tab. 3) and in most (81.4 %) of the pitfall traps on the upland side of the fences in year one. Upland side captures occurred during three distinct periods of migration, all of which were immigration events. These migration events (I1, I2 and I3, tab. 4) occurred during the same time periods as described above for pond-side captures (tab. 4). Immigration event I3 accounted for the largest proportion (54 %) of upland-side captures in year one, followed by event I1 (29 %) and I2 (17 %). All of these migration events consisted of adult newts moving toward OSP to breed (tab. 4).

I captured 495 newts in the upland drift fences during year two (fig. 3b, tab. 3). In contrast to year one, migration consisted primarily of immigrating adults. Pond-side captures accounted for only 9 % of total captures. I captured newts at each of the two fence sections (fig. 3b) and at each distance from OSP (tab. 3), but captures were recorded in less than half of the pitfall traps (42.8 %) on the pond-side of the upland fences in year two. Pond-side captures at

Table 4   Captures of striped newts in upland fences around One Shot Pond, Putnam Co., Florida, USA, during distinct periods of movement *: fence arrays modified in early December 97

Fence side of captures	Migration event	Predominant direction of newt movement	Time period of event	Number of newts captured	Description
Year 1					
Pond-side	E1	Away from pond	October 96 through February 97	461	Emigrating efts
Pond-side	E2	Away from pond	April 97 through July 97	91	Primarily emigrating paedomorphs and efts
Pond-side	I3	Toward pond	October 97 through December 97*	55	Immigrating adults
Upland-side	I1	Toward pond	October 96 through January 97	65	Immigrating adults, some emigrating efts
Upland-side	I2	Toward pond	April 97 through July 97	36	Immigrating adults
Upland-side	I3	Toward pond	November 97 through December 97*	123	Immigrating adults
Year 2					
Pond-side	I3	Toward pond	December 97* through March 98	16	Immigrating adults
Pond-side	E3	Away from pond	June 98 through September 98	25	Emigrating efts
Upland-side	I3	Toward pond	December 97* through March 98	449	Immigrating adults

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upland fences in year two represented two distinct periods of newt migration, one immigration event (i.e., I3) and one emigration event (i.e., E3). I captured few newts during both of these events; 16 during I3 and 25 newts during E3 (tab. 4). Captures during migration event I3 were adults that were moving to the pond to breed but were captured in pond-side traps as they wandered toward the pond. Captures during E3 were recently transformed newts that were leaving OSP.

In year two, I captured far more newts (91 % of total upland captures) on the upland-side of drift fences than on the pond-side (tab. 3). I captured newts at all sections of drift fence and in almost all of the upland-side pitfalls (88.6 %). Captures occurred during a single immigration event (I3; tab. 4) and were exclusively of adults that were immigrating to OSP to breed. The number of captures declined as the distance from the pond increased (tab. 3). Based on estimated values, at least 360 newts (16 % of the breeding migration) migrated more than 500 m from OSP (fig. 6). I estimated that 645 newts (29 % of the breeding migration) migrated at least 400 m. The estimate was the same for 300 m (645 newts). I estimated that 810 (36 % of the breeding migration) and 908 (41 % of the breeding migration) of newts migrated from the pond at least 200 and 100 m, respectively (fig. 6). Based on these estimates, it appears that roughly 60 % of the striped newts emigrated less than 100 m. However, as indicated by captures at the 500 m fences, a substantial percentage of individuals comprising the 1997-98 breeding migration immigrated to OSP from farther than 500 m. In fact one newt that was marked leaving OSP as an eft on 18 November 1996 was recaptured on 4 February 1998 as it colonized Fox Pond, a dispersal distance of approximately 685 m.

DISCUSSION

ORIENTATION

The distribution of habitats surrounding a breeding pond should influence patterns of immigration revealed by captures of salamanders at the pond. Habitat preferences among species and/or differential survivorship in various habitat types might be apparent as individuals arrive at the breeding pond. For example, imagine an amphibian breeding-pond in which one half of the uplands surrounding the pond were pine plantation (i.e., marginal habitat) whereas the other half remained native uplands (i.e., preferred habitat). The pattern of captures at the pond would be expected to reflect the distribution of upland habitats. One might predict significantly fewer captures along the half of the pond adjacent to the pine plantation as compared to the native upland half. This is because pond-breeding salamanders have the ability to select appropriate upland habitats and accurately navigate through uplands during migration, often using specific habitat types (SHOOP, 1968, HURLBERT, 1969; SEMLITSCH, 1981, STENHOUSE, 1985; MADISON, 1997; MADISON & FARRAND, 1998, DI MAYNADIER & HUNTER, 1999, MALMGREN, 2002, ROTHERMEL & SEMLITSCH, 2002)

In this study, although newts entered and exited the pond basin from all directions, migration was nonrandom. Some directions were preferred over others, but there were no obvious upland habitat features that could explain the newts' orientation behavior. However, I did not measure habitat variables in the uplands and individuals could have used micro-
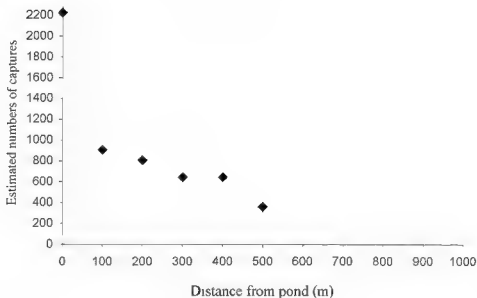
Fig. 6   Estimated numbers of striped newt captures in pitfall traps at drift fences in the sandhill uplands around One Shot Pond, Putnam Co., Florida, USA. Drift fences were located at 100 m intervals up to 500 m from the pond. The zero point represents captures at a drift fence encircling the pond. See *Materials and methods* for an explanation of how the estimated numbers were calculated.

topographic features as cues to navigate toward the pond. In a similar study, DODD & CADE (1998) concluded that movements of striped newts and narrowmouth toads were a reflection of the distribution of favorable upland habitats around the pond. Although the uplands at OSP were primarily sandhill habitat, a small plantation of slash pine (with intact groundcover) was well within the dispersal capabilities of migrating newts (fig. 2). In year one I often caught newts at a section of drift fence in the pine plantation. Newts could have resided within the plantation or have traveled through it en route to native sandhill. Nevertheless, this plantation represented only a small portion of the uplands and had no detectable effect on striped newt movements.

Although upland-habitat preferences and microenvironmental features I did not measure could have influenced the nonrandom pattern of immigration observed at OSP, if measured over several seasons, orientation may in fact be random. It is possible that striped newts are roughly evenly distributed in the uplands around OSP but that only a portion of the population migrates to the pond during any particular breeding event. If the portion of individuals moving was not indicative of the whole population, then what truly should be random orientation would appear as nonrandom because data were collected for a relatively short time.

Patterns of newt emigration were also nonrandom, and newts exited the pond basin in all directions. Efts emigrated predominantly in the southwest quadrant of the pond. The slope of the pond basin was shallowest in this quadrant, and water depth during metamorphic events

could have influenced the behavior of recently transformed efts as they left the pond. On the other hand, adults emigrated most often in the south-southeast portion of the basin. Differences in aquatic habitat preference (e.g., depth) between adult and immature newts might explain the varying emigration patterns, although habitat preferences of both life history stages are unknown.

UPLAND MIGRATION

Using upland drift fence arrays in year two, I was able to estimate the percentage of the striped newt breeding population that migrated different distances (in increments of 100 m) from the pond. Captures at drift fences in the sandhill uplands surrounding OSP indicated that many striped newts (16 %) migrated more than 500 m from the pond. This is a conservative estimate because newts captured in traps closer to the pond may have migrated further than indicated by the traps. Captures at the drift fence surrounding the pond and at upland drift fences at the end of year one showed that a breeding migration of newts into OSP had begun before the installation of fences for year two (JOHNSON, 2001, 2002). Although the proportion of individuals caught at the pond before the new upland fence arrays were established was small (7 % of the total), some newts already had moved toward the pond before the upland arrays were in place. Moreover, immigrating adults did not arrive at the pond in a random fashion during this breeding migration. The upland fence arrays in year two were located north and southeast of OSP and newts were caught at the pond with lowest frequency toward the north. Therefore, the proportion of the breeding population caught at each distance from the pond in year two is likely an underestimate of the actual proportion that migrated to that particular distance.

Many pond-breeding amphibians spend and spend much of their adult lives in terrestrial habitats away from breeding sites. Distances that individuals disperse or migrate from breeding ponds have been reported for some species (DODD, 1996; SEMLITSCH, 1998 and references therein). It is clear that individuals disperse and migrate hundreds of meters from breeding sites into upland habitats, some even thousands of meters. With few exceptions, however, distance values usually have been presented for less than 10 individuals per species. The results from my study appear to be the first estimates of migration distances for a breeding population of North American amphibians based on a substantial sample size.

CONSERVATION IMPLICATIONS

Central to a successful amphibian conservation strategy is the protection of sufficient breeding and nonbreeding habitat (i.e., the pond and appropriate "core habitat", SEMLITSCH & JENSEN, 2001) Studies of amphibian migration and dispersal can provide the scientific basis for determining directional and distance components that can be used to establish protected areas around breeding ponds. BROWN et al. (1990) used spatial requirements (i.e., distance moved from a wetland), among other data, to recommend width of "buffer zones" for wildlife protection at wetlands in Florida. Nevertheless, lack of data for amphibians forced them to use rough estimates for most of the species considered. Further utility of movement distance data can be found in regulations to protect the flatwoods salamander (*Ambystoma cingula-*

tum) which, as a result of severe population decline (MEANS et al., 1996), was federally listed as threatened in the USA (ANONYMOUS, 1999). The US Fish and Wildlife Service restricts specific silvicultural practices within 450 m of flatwoods salamander ponds. Additionally, only selective timber harvest at specific times is allowed within a primary radius of 164 m around breeding ponds (ANONYMOUS, 1999). The width of the primary zone (164 m) was derived from a review of migration distances for pond-breeding salamanders of the genus *Ambystoma* (SEMLITSCH, 1998), despite the fact that no data for *A. cingulatum* were presented. This example underscores the need to determine migration and dispersal distances for all pond-breeding amphibians. SEMLITSCH (1998) acknowledged that the extent of protected upland recommended for *Ambystoma* species may apply to some species of pond-breeding amphibians, but certainly not all. My data show that recommendations for protecting terrestrial habitat for ambystomatid salamanders are inadequate for *Notophthalmus perstriatus*. Therefore, it is not defensible to extrapolate data across taxa. Clearly, a 164 m protected zone would not protect all of the striped newts breeding at OSP. Based on extrapolation of migration distances revealed by upland drift fences, a protected area of "core habitat" extending ca. 1000 m from OSP would likely be needed to encompass almost all of the newts that breed there.

Although they have great value as wildlife habitat, small, isolated wetlands in the United States are afforded little protection from development. Overall, more than 50 % of wetlands have been destroyed by development in the United States (DAHL, 1990), and much of this loss has been small wetlands. In Florida, a state with an extremely large number and diversity of wetlands, isolated wetlands less than 0.2 ha receive no protection from development. This size threshold was adopted by the state's water management districts "based on a consensus of scientific and regulatory opinion rather than on biological and hydrological evidence" (HART & NEWMAN, 1995). Small wetlands are just as vulnerable at the national level as they are in Florida.

There is strong evidence that protection of core areas of terrestrial habitat surrounding breeding sites is crucial for persistence of amphibian populations and species. Data from OSP demonstrate that small, isolated wetlands can support breeding populations of salamanders that migrate hundreds of meters into the surrounding uplands. Similar studies at other ponds and in different upland types are necessary because data on upland habitat requirements (quality and quantity) of most amphibian species are lacking. Without this information, designating terrestrial "core habitat" to conserve aquatic-breeding amphibians will largely remain guesswork, with generalizations made from data on relatively few individuals of a few species. However, unless more protection is afforded to small, isolated wetlands, arguments to preserve uplands surrounding the wetlands are irrelevant.

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Revision of the genus *Ophryophryne*
Boulenger, 1903 (Megophryidae)
with description of two new species

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Study of type specimens and newly collected specimens of frogs of the oriental genus *Ophryophryne* Boulenger, 1903 lead to the redefinition of the recognized taxa and the recognition of two new species, one reported from Vietnam and Laos, and the second only from Vietnam. *Ophryophryne poilani* Bourret, 1937 is put to the synonymy of *Ophryophryne microstoma* Boulenger, 1903. The range of the species *O. microstoma*, which includes Vietnam and China, is extended to Thailand. *Ophryophryne pachyproctus* Kou, 1985 is confirmed by a new specimen from Vietnam.

Ophryophryne Boulenger, 1903 is a member of the family Megophryidae Bonaparte, 1850 as defined by FORD & CANNATELLA (1993). Sister-group of *Xenophrys* Günther, 1864 as defined by DUBOIS & OHLER (1998), it is either regarded as a separate genus (recent references: YE et al., 1993, MANTHEY & GROSSMANN, 1997) or as a subgenus of *Megophrys* Kuhl & Van Hasselt, 1822 (DUBOIS, 1980)

The genus *Ophryophryne* was described in 1903 by BOULENGER (1903a) who mentioned both its close morphological resemblance to *Megophrys*, and its lack of maxillary and vomerine teeth and the presence of a horizontal pupilla, characters defining the family Bufonidae Gray, 1825 Although BOULENGER (1903a) was aware of the problem of using isolated characters in making taxonomic decisions, he included his new genus into the Bufonidae (BOULENGER, 1903b). Despite the work of NOBLE (1926), who clearly recognized this genus as a member of the Pelobatidae (including then the subfamily Megophryinae), close to the genus *Megophrys*, most authors continued to consider it to be a member of the Bufonidae (see review in DUBOIS, 1980: 470, recent reference, NGUYEN & HO, 1996) The description of the tadpole (LIU & HU, 1962) and the study of external morphology indicated *Ophryophryne* to be a megophryid and closely related to *Megophrys* (DUBOIS, 1980). Recent studies based on cytology and adult and larval morphology confirmed *Ophryophryne* to be the sister-group of *Xenophrys*, a group formerly included in the genus *Megophrys* (TIAN & HU, 1985. 220; RAO & YANG, 1997; DUBOIS & OHLER, 1998).

The genus was described to include one species, *Ophryophryne microstoma* Boulenger, 1903. In 1937, BOURRET described a second species, *Ophryophryne poilani*, based upon a single, badly preserved specimen. Not until 1985 was a third species described by KOU, *Ophryophryne pachyproctus* from southern China (Yunnan).

In recent years important new material of amphibians was collected in South-East Asia. INGER et al. (1999) reported on the three species of *Ophryophryne* from southern Vietnam. Beside the material collected in Vietnam, I had the opportunity to study the type-specimens of the three nominal species and other material stored in museum collections. The analysis of these data led me to describe two new species in this genus and to put *Ophryophryne poilani* in the synonymy of *Ophryophryne microstoma*.

MATERIALS AND METHODS

The material studied is listed under the appropriate species and is deposited in the museums mentioned below. My study is based on morphology and morphometry of formalin-fixed and alcohol-preserved specimens. Data on live animals are added when available. The descriptions, methodology and terminology follow OHLER (1996) and DUBOIS & OHLER (1998). The webbing formula used is that of MYERS & DUELLMAN (1982). All measurements are in millimetres. The tables present measurements and their per mille ratios to SVL (in brackets) with the associated mean and standard deviation. Abbreviations for measurements and institutions are as follows:

SVL, snout-vent length.

Head. HW, head width; HL, head length (from posterior edge of mandible to tip of snout); MN, distance from posterior edge of mandible to posterior border of nostril; MFE, distance from posterior edge of mandible to anterior corner of eye; MBE, distance from posterior edge of mandible to back of eye; IFE, distance between anterior corner of eyes; IBE, distance between posterior border of eyes; IN, internarial space; EN, distance from anterior corner of eye to posterior border of nostril; EL, eye length; SN, distance from anterior corner of nostril to tip of snout; SL, distance from front of eye to tip of snout; TYD, greatest tympanum diameter; TYE, smallest distance from anterior border of tympanum to posterior corner of eye; IUE, minimum distance between upper eyelids; UEW, maximum width of inter upper eyelid.

Forearm. HAL, hand length (from base of outer palmar tubercle to tip of toe); FLL, forelimb length (from elbow to base of outer tubercle); TFL, third finger length (from base of first subarticular tubercle).

Hindlimb. FL, femur length (from vent to knee); TL, tibia length; FOL, foot length (from base of inner metatarsal tubercle to tip of toe); FTL, foot length (from base of first subarticular tubercle); TFOL, distance from base of tarsus to tip of fourth toe.

Webbing. MTTF, distance from distal edge of metatarsal tubercle to maximum incurvation of web between third and fourth toe; TFTF, distance from maximum incurvation of web between third and fourth toe to tip of fourth toe; MTFF, distance from distal edge of

metatarsal tubercle to maximum incurvation of web between fourth and fifth toe; FFTF, distance from maximum incurvation of web between fourth and fifth toe to tip of fourth toe.

nm, not measured

p.m., per mille.

BMNH, Natural History Museum, London, United Kingdom.
CIB, Chengdu Institute of Biology, Chengdu, Sichuan, China.
FMNH, Field Museum of Natural History, Chicago, Illinois, USA.
IEBR, Institute of Ecology and Biological Research, Hanoi, Vietnam.
MNHN, Muséum national d'Histoire naturelle, Paris, France
YU, Yunnan University, Kunming, Yunnan, China.

TAXONOMIC ACCOUNTS

Ophryophryne Boulenger, 1903

Ophryophryne Boulenger, 1903 186   Type-species *Ophryophryne microstoma* Boulenger, 1903, by monotypy

Ophryophryne gerti sp. nov.

Holotype. – BMNH 1921.4.1.324, adult male, Cam Ly (river), south-east of Da Lat (11°56'N, 108°25'E), Lang Bian Plateau, sLam Dong Province, Vietnam.

Paratypes BMNH 1921 4.1.323, young female, Dran (11°50'N, 108°34'E), Lang Bian Plateau, Lam Dong Province, Vietnam; BMNH 1972.15.2 4, adult male, Huey Sapan, Pak Maat (precise location not found), Mekong, Laos.

Other specimens examined. – VIETNAM· Buon Luoi, An He District, Gia-Lai Province· FMNH 252899, 252901.

Diagnosis Small-sized *Ophryophryne*, with relatively long tibia, small tympanum, small head Dorsal coloration uniform, dark. Supraorbital horn distinct, no dermal protuberance bearing anus

Description of holotype (fig 1). – (A) Size and general aspect   (1) Specimen of rather small size (SVL 34.8 mm); body slender.

(B) Head   (2) Head small, wider (HW 9 1 mm) than long (HL 8.5 mm. MN 7 5 mm; MFE 6 5 mm, MBE 3 4 mm), convex. (3) Snout truncate, protruding, its length (SL 3 31 mm) shorter than horizontal diameter of eye (EL 3 95 mm). (4) Canthus rostralis rounded, loreal region slightly convex, acute in cross section (5) Interorbital space concave, narrower (IUE 2 59 mm) than upper eyelid (UEW 2 98 mm) and than internarial distance (IN 3 05 mm); distance between front of eyes (IFE 5 31 mm) about two third of distance between back of eyes (IBE 7 9 mm) (6) Nostrils oval, with small flap of skin laterally, closer to eye (EN 1 23 mm) than to tip of snout (NS 1 62 mm) (7) Pupil rounded (in preservative). (8) Tympanum (TYD 2 14 mm) rounded. about half eye diameter and approximately equal to

Fig. 1 – *Ophryophryne gerti* sp. nov. BMNH 1921.4.1.324, holotype, adult male, SVL 34.8 mm. Dorsal view (top); lateral view of head (bottom).

tympanum-eye distance (TYE 2.07 mm) (9) Pineal ocellus absent. (10) Vomerine ridge absent. (11) Tongue rounded, with dorsal hollow, largely attached to mouth floor. (12) Supratympanic fold prominent, from eye to shoulder.

(C) Forelimbs. (13) Arm rather long, fore-arm (FLL 8.6 mm) longer than hand (HAL 8 0 mm), not enlarged. (14) Fingers I, II and IV short and thin; finger III long and thin (TFL 4.99 mm). (15) Relative length of fingers, shortest to longest: I < II = IV< III. (16) Tips of fingers rounded, not enlarged. (17) Fingers without dermal fringe; webbing absent. (18) Subarticular tubercles absent. (19) Prepollex oval, indistinct; palmar tubercles indistinct and supernumerary tubercles absent.

(D) Hindlimbs. - (20) Shanks three times longer (TL 15.4 mm) than wide (TW 4 8 mm), about same length as thigh (FL 15.2 mm) and longer than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 14 8 mm). (21) Toes long and thin, toe IV (FTL 7 0) about third of distance from base of tarsus to tip of toe IV (TFOL 21 4 mm) (22) Relative length of toes, shortest to longest: I < II < III < IV. (23) Tips of toes rounded, not enlarged (24) Webbing absent. I 2 - 2 ½ II 2 - 3 III 2 ½ 4 IV 4 2 ½ V (MTTF 3.95 mm, MTFF 4 61 mm; FTTF 6 97 mm; FFTF 6 97 mm). (25) Dermal fringe along toe V absent (26) Subarticular tubercles absent. (27) Inner metatarsal tubercle flat, its length (IMT 2.07 mm) 1 16 times in length of toe I (ITL 2.40 mm). (28) Tarsal fold absent (29) Outer metatarsal tubercle, supernumerary tubercles and tarsal tubercle absent.

(E) Skin. (30) Dorsal and lateral parts of head and body: snout shagreened, granular, between eyes smooth and shagreened; side of head granular, orbital horn free, pointed, its length 0 78 mm, anterior part of back shagreened; posterior part of back shagreened, granular; upper part of flank shagreened, with glandular warts, lower part of flank granular (31) Cephalic ridges absent. (32) Latero-dorsal folds, lateral line system and "Fejervaryan" line absent. (33) Dorsal parts of limbs: forelimb smooth, with few small glandular warts; thigh and leg with flat glandular warts, tarsus smooth. (34) Ventral parts of head, body and limbs: throat, chest, belly and thigh smooth. (35) Small pairs of pectoral and femoral glands present.

(F) Coloration in alcohol. (36) Dorsal and lateral parts of head and body dorsal parts of head and dorsum and upper part of flank dark brown, homogeneous, lower parts of flank with darker brown spots; loreal region brown with darker brown indistinct bands including upper lip, tympanum and tympanic region dark brown, tympanic fold underlined by blackish brown. (37) Dorsal parts of limbs. dorsal part of forelimbs, of thigh, of shank and of foot dark brown with indistinct darker brown bands, posterior part of thigh brown with blackish triangle around vent (38) Ventral parts of head, body and limbs: throat, margin of throat, chest and thigh rather dark brown, lower part of belly yellow with brown spots and blackish spots, dark brown spots also on ventral part of thighs; macroglands white

Coloration in life. - Not known.

(G) Male secondary sexual characters. (39) Nuptial spines present on fingers I and II, numerous small brown spines forming two oval patches. (40) Vocal sacs absent, non visible either exteriorly or interiorly. (41) Other male secondary sexual characters. dorsally of vent, presence of a short fleshy flap.

Female sexual characters. – Not observed.

Table 1.   Measurements (mm) and per mille of snout-vent length (in parenthesis) of five specimens,
including holotype, of *Ophryophryne gerti* sp. nov.

Collection number	BMNH 1921.4.1.324	BMHN 1972.15.2.4	BMNH 1921.4.1.323	FMNH 252899	FMNH 252901
Locality	Cam Ly, Vietnam	Huey Sapan, Laos	Dran, Vietnam	Buon Luoi, Vietnam	Buon Luoi, Vietnam
Status	Holotype	Paratype	Paratype	Additional material	Additional material
Sex	Adult male	Adult male	Juvenile female	Adult female	Adult female
Snout-vent length	34.8	32.0	21.0	41.4	45.8
Head length	8.5 (244)	8.5 (266)	6.4 (305)	11.0 (266)	11.2 (245)
Tympanum diameter	2.01 (58)	2.13 (67)	1.16 (55)	2.92 (71)	3.24 (71)
Thigh	15.2 (437)	15.6 (488)	8.7 (414)	nm	nm
Shank	15.4 (443)	15.5 (484)	9.3 (443)	17.4 (420)	18.0 (393)
Foot	14.8 (425)	13.4 (419)	7.3 (.348)	16.8 (406)	16.9 (369)

Variation.   A second male is smaller in body size (tab. 1), but very similar in all body
measurements. Its nuptial pads are translucent, which might indicate that he is sub-
adult.

Distribution – *Ophryophryne gerti* is known from Laos and Vietnam.

Etymology   This species is dedicated to my sister Gerti for her help during fieldwork. The
invariable specific epithet *gerti* is a noun used in apposition.

Comments.   Two female specimens (FMNH 252899, 252901) from Buon Luoi (Vietnam) are
here tentatively referred to this species. These specimens are distinguished by smooth skin.
Skin is in general smoother in female than in male specimens in *Ophryophryne*. As these
females are morphologically distinct from the three other species of the genus, but show
similarities to the type-specimens of *O. gerti*, they are included in this species.

Ophryophryne hansi sp. nov

Ophryophryne poilani (non Bourret, 1937: 8): INGER et al., 1999: 9.

Holotype   FMNH 252880, adult male, Buon Luoi (700-750 m), 20 km west of the town of
Kannack (14°20'N, 108°36'E), An Khe District, Gia-Lai Province, Vietnam (INGER et al.,
1999).

Paratopotypes   FMNH 252873, 252875, 252878-79, 252882, 252884, 252892-93, 7 adult
males, 1 adult female.

Diagnosis   Relatively large-sized *Ophryophryne*, with relatively long shank, small tympa-
num, large head. Dorsal coloration dark, almost black. Supraorbital horn forming small
projection, no dermal protuberance bearing anus.

Description of holotype (fig. 2).   (A) Size and general aspect   (1) Specimen of medium size
(SVL 38.8 mm), body rather stout

     (B) Head   (2) Head very small, wider (HW 12.4 mm) than long (HL 10.4 mm; MN
9.3 mm; MFE 8.1 mm, MBE 4.0 mm), convex (3) Snout rounded, very protruding, its length

Fig 2 *Ophryophryne hansi* sp. nov. FMNH 252880, holotype. adult male. SVL 38 8 mm. Dorsal view (left); ventral view (right).

(SL 3 76 mm) shorter than horizontal diameter of eye (EL 4 86 mm) (4) Canthus rostralis rounded, loreal region concave, acute in cross section (5) Interorbital space convex, narrower (IUE 2 72 mm) than upper eyelid (UEW 3 76 mm) and internarial distance (IN 3.04 mm), distance between front of eyes (IFE 6 0 mm) three fifth of distance between back of eyes (IBE 10 0 mm) (6) Nostrils oval, with small flap of skin laterally, closer to eye (EN 1 43 mm) than to tip of snout (NS 1 69 mm) (7) Pupil diamond-shaped, vertical (8) Tympanum (TYD 2 14 mm) distinct, oval, vertical, smaller than half diameter of eye, tympanum-eye distance (TYE 2 46 mm) more than its diameter (9) Pineal ocellus absent (10) Vomerine ridge absent. (11) Tongue large, rounded, not emarginate (12) Supratympanic fold distinct, present from eye to shoulder, posterior part slightly enlarged

(C) Forelimbs. (13) Arm long, thin, fore-arm (FLL 9.7 mm) shorter than hand (HAL 10.9 mm), not enlarged. (14) Fingers long and thin (TFL 5.7 mm). (15) Relative length of fingers, shortest to longest: I < II < IV < III. (16) Tips of fingers rounded, not enlarged. (17) Fingers without dermal fringe; webbing absent. (18) Subarticular tubercles indistinct; on fingers I and II a single proximal, oval tubercle. (19) Prepollex oval, indistinct, a single, oval palmar tubercle; supernumerary tubercles absent.

(D) Hindlimbs. (20) Shanks four times longer (TL 18.9 mm) than wide (TW 4.9 mm), about length of thigh (FL 18.7 mm), but longer than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 16.9 mm). (21) Toe IV (FTL 9.1) about one third of distance from base of tarsus to tip of toe IV (TFOL 26.7 mm). (22) Relative length of toes, shortest to longest: I < II < V < III < IV. (23) Tips of toes rounded, slightly enlarged; discs absent. (24) Webbing absent: I 2⁻ 2 ½ II 2⁻ 3 ¼ III 3⁻ 3 ½ IV 3 ½⁻ 2 ½ V (MTTF 5.53 mm; MTFF 6.32 mm; FTTF 10.40 mm, FFTF 10.40 mm). (25) Dermal fringe along toe V absent. (26) Subarticular tubercles indistinct. (27) Inner metatarsal tubercle long, flat, its length (IMT 3.37 mm) 1.06 times in length of toe I (ITL 3.57 mm). (28) Tarsal fold absent. (29) Outer metatarsal tubercle, supernumerary tubercles and tarsal tubercle absent.

(E) Skin. (30) Dorsal and lateral parts of head and body: snout, between eyes, side of head, back and upper part of flanks with glandular warts and horny spinules, on lower part of flank, some of these warts of large size. (31) Dorsal parts of limbs absent. (32) Latero-dorsal folds, lateral line system and "Fejervaryan" line absent. (33) Dorsal parts of limbs: forelimb, thigh, leg and tarsus with glandular warts and horny spinules. (34) Ventral parts of head, body and limbs: throat, chest with foldings; belly and thigh smooth. (35) Femoral and pectoral glands present; medium sized glands on flanks and rear part of thigh.

(F) Coloration in alcohol. (36) Dorsal and lateral parts of head and body: dorsal parts of head and dorsum grey-brown with dark brown spots, in particular a triangle between eyes, flanks grey-brown with dark brown and white spots, white ones corresponding to glands; loreal region dark brown, tympanum and tympanic region dark brown with a light brown stripe from eye to upper lip, upper lip dark brown with few clear spots. (37) Dorsal parts of limbs: dorsal part of forelimbs, of thigh, of shank and of foot grey-brown with broad dark brown bands; posterior part of thigh brown with dark perianal zone and dark zone around femoral glands; femoral glands and glands near vent whitish. (38) Ventral parts of head, body and limbs: throat and margin of throat brown with dark brown spots, chest brown with dark brown spots and whitish pectoral glands, belly and thigh yellowish with brown marblings, pectoral glands whitish.

Coloration in life. "In life males vary from black with sharply delimited yellow spots to grey brown with obscure lighter spots; females yellowish grey with obscure, small lighter spots" (INGER et al., 1999: 9).

(G) Male secondary sexual characters. (39) Numerous, small, dark brown nuptial spines forming oval pads on fingers I and II. (40) Single vocal sac present, with rounded openings posterior on mouth floor. (41) Other male secondary sexual characters: fleshy flap on vent not present

Female sexual characters (FMNH 252882, SVL 53.5 mm). Large (2.40 mm) creamy-whitish ovocytes in ovary

Table 2 – Measurements (mm) and per mille of snout-vent length (in parenthesis) of type-specimens of *Ophryophryne hansi* sp. nov., from Buon Luoi Vietnam Means and standard deviations are given between square brackets. Thigh was not measured in these specimens.

Collection number	FMNH 252880	FMNH 252873, 252875, 252878-79, 252884, 252892-93	FMNH 252882
Status	Holotype	7 paratypes	Paratype
Sex	Adult male	Adult males	Adult female
Snout-vent length	38.8	35 3-43.0 [38.8 ± 2 51]	53.5
Head width	12.4 (320)	11 3-12.9 (291-347) [12 3 ± 0.54 (319 ± 20 9)]	15 8 (295)
Head length	10 4 (268)	10.6-11.7 (258-315) [11.1 ± 0.35 (286 ± 20 1)]	14.5 (271)
Tympanum diameter	2 (52)	2 59-2 92 (63-74) [2 72 ± 0 14 (70 ± 4.3)]	3 6 (68)
Shank	18 9 (487)	18.4-19 0 (440-538) [18 9 ± 0.22 (488 ± 33 9)]	25 6 (479)
Foot	16 9 (436)	16 1-18.2 (395-478) [16 8 ± 0 69 (435 ±31·0)]	23 9 (447)

Variation. – Table 2 gives variation of body measurements for males and female.

Distribution. – Species known only from the type-locality in Vietnam.

Etymology. This species is dedicated to my sister Hansi who very kindly "adopts" my son during periods of fieldwork, thus generously supporting my research. The invariable specific epithet *hansi* is a noun used in apposition.

Ophryophryne microstoma Boulenger, 1903

Ophryophryne microstoma Boulenger, 1903a: 186 – *Type-specimen* lectotype, by present designation, BMNH 1947 2.22 52 [ex 1903 4 29 106], adult male (exam.ned) *Type-locality* Mau Son ["Man-Son Mountains, Tonkin, altitude 3000-4000 feet"] (22°00'N, 106°45'E), Lang Son Province, Vietnam
   Megophrys (Ophryophryne) microstoma: DUBOIS, 1980: 473
   Ophryophryne microstoma: DUBOIS, 1987: 23.
Ophryophryne poilani Bourret, 1937 8 – *Type-specimen* holotype, by monotypy, MNHN 1948 0113, adult female (examined) *Type-locality* Dong-Tam-Ve (16°40'N, 106°45'E), concession of the collector E. Poilane near the Atlao Pass, Quang Tri Province, Vietnam *New synonym*
   Megophrys (Ophryophryne) poilani: DUBOIS, 1980: 472
   Ophryophryne poilani. DUBOIS, 1987: 23

Other specimens examined – THAILAND NE Thailand BMNH 1974 2334 (hands and limbs missing). VIETNAM: Man Son Mountains, Tonkin, 3000-4000 feet BMNH 1947 2 22 50-51 [ex 1903 4 29 104-105], 1947 2 22.53 [ex 1903 4 29 107], Ben En, Tanh Hoa province MNHN 1997.5258-5260, IEBR D.231; Tam Dao, Viet Tri FMNH 254250-254251. MNHN 1997.4931-4933

Diagnosis. An *Ophryophryne* of relatively large size, with relatively short shank, moderate-sized tympanum, small head. Dorsal coloration ochre, rather clear, with distinct pattern Supraorbital horn distinct, no dermal protuberance bearing anus.

Description of the lectotype (fig. 3) – (A) Size and general aspect – (1) Specimen of medium size (SVL 39.1 mm), body elongate
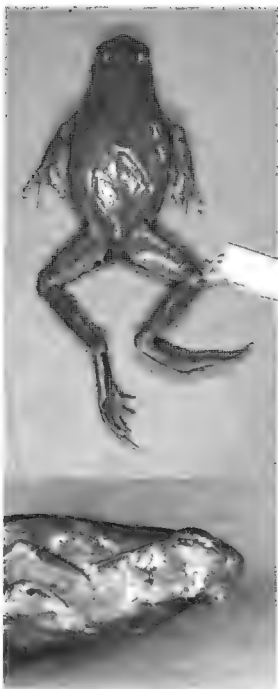
Fig. 3. *Ophryophryne microstoma* Boulenger, 1903. BMNH 1947.2.22.52, lectotype, adult male, SVL 39.1 mm. Dorsal view (top); lateral view of head (bottom).

(B) Head   (2) Head very small, as wide (HW 9.5 mm) as long (HL 9.4 mm, MN 8.0 mm; MFE 7.0 mm, MBE 4.6 mm), convex. (3) Snout truncate, protruding; its length (SL 3 56 mm) shorter than horizontal diameter of eye (EL 4.54 mm). (4) Canthus rostralis rounded, loreal region concave, acute in cross section (5) Interorbital space convex, narrower (IUE 2.53 mm) than upper eyelid (UEW 3.37 mm) and than internarial distance (IN 3.05 mm); distance between front of eyes (IFE 5 6 mm) about two thirds of distance between back of eyes (IBE 8.8 mm). (6) Nostrils oval, with small flap of skin laterally, at equal distance to tip of snout (NS 1.62 mm) and to eye (EN 1 56 mm). (7) Pupil indistinct, shape not visible. (8) Tympanum (TYD 2.59 mm) rounded, rather distinct, more than half eye diameter; tympanum-eye distance (TYE 1.94 mm) two thirds of its diameter. (9) Pineal ocellus absent. (10) Vomerine ridge absent. (11) Tongue moderate, rounded, thick, emarginate, adhering largely to mouth floor (12) Supratympanic fold prominent, present from eye to shoulder.

(C) Forelimbs. – (13) Arm rather long, fore-arm (FLL 9.5 mm) not enlarged, longer than hand (HAL 9 2 mm) (14) Fingers I, II and IV short and thin; finger III long and thin (TFL 5.57 mm). (15) Relative length of fingers, shortest to longest: I < II = IV< III (16) Tips of fingers rounded, not enlarged, without distinct grooves. (17) Fingers without dermal fringe, webbing absent. (18) Subarticular tubercles absent (19) Prepollex oval, distinct; palmar tubercles indistinct; supernumerary tubercles indistinct

(D) Hindlimbs. – (20) Shanks four times longer (TL 16.0 mm) than wide (TW 3 9 mm), longer than thigh (FL 15.8 mm) and than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 15 4 mm). (21) Toe IV (FTL 7.4) about one third of distance from base of tarsus to tip of toe IV (TFOL 23 3 mm) (22) Relative length of toes, shortest to longest: I < II < V < III < IV. (23) Tips of toes rounded, not enlarged, without distinct grooves. (24) Webbing absent: I 2 – 2 ½ II 2 – 3 III 3 – 4 IV 4 – 3 V (MTTF 4.47 mm; MTFF 5 39 mm; FTTF 7.89 mm; FFTF 8 03 mm). (25) Dermal fringe along toe V absent (26) Subarticular tubercles absent. (27) Inner metatarsal tubercle indistinct, its length (IMT non measurable, about 2 mm) 1 4 times in length of toe I (ITL about 2 8 mm). (28) Tarsal fold absent (29) Outer metatarsal tubercle, supernumerary tubercles and tarsal tubercle absent.

(E) Skin   (30) Dorsal and lateral parts of head and body. snout, between eyes, side of head and back shagreened, upper and lower part of flank shagreened covered with granules. (31) Cephalic ridges absent (32) Latero-dorsal folds, lateral line system and "Fejervaryan" line absent. (33) Dorsal parts of limbs. forelimb, thigh, leg and tarsus shagreened, with granules. (34) Ventral parts of head, body and limbs: throat, chest, belly and thigh smooth (35) Pectoral glands, femoral glands and glandular tympanic fold present

(F) Coloration in alcohol.   (36) Dorsal and lateral parts of head and body. dorsal parts of head and dorsum and upper part of flank dark ochre, homogeneous, dorsal folds with some small darker spots. lower part of flank beige with ochre spots and some dark brown spots, loreal and tympanic regions dark ochre, tympanum transparent, upper lip dark ochre. (37) Dorsal parts of limbs. dorsal parts of forelimbs. of thigh, of shank and of foot ochre with darker bands, posterior part of thigh ochre with distinct dark brown spots. (38) Ventral parts of head, body and limbs ground light yellow, almost entirely covered by ochre on throat, chest and upper vent, with large ochre flecks on central part of belly, leaving light yellow ground out; posterior part of vent light ochre; thigh light yellow with dense ochre spots, webbing ochre; macroglands whitish.

Coloration in life (specimen IEBR D231). Dorsal parts of head and dorsum ochre, with darker brown grey pattern and sand colored crests. Flanks brown grey and sand colored with black spots, inferior part with white warts. Loreal region coppery brown, iris copper colored with network of melanophores, tympanic region anteriorly dark reddish brown and posteriorly coppery brown, tympanum coppery brown, upper lip continuous with other parts of side of head. Forelimbs, dorsal part of thigh, dorsal part of leg and foot brown grey and sand color with black spots. Posterior part of thigh dark and whitish grey with brownish spots and white warts; femoral glands ivory. Throat brownish, chest coppery brown with ivory colored pectoral glands, belly coppery brown with white spots anteriorly, and whitish grey with dark brown spots in its posterior part. Ventral side of thigh whitish grey with brown spots.

(G) Male secondary sexual characters. (39) Traces indicate that nuptial spines have been present on fingers I and II, with spines small, numerous. (40) Vocal sacs not observed (to preserve holotype). (41) Other male secondary sexual characters: dorsally of vent, presence of a small fleshy flap.

Female sexual characters (adult female MNHN 1997.5259) Large glandular circumvoluted oviduct; creamy white, small sized, immature ovocytes (this female probably just laid eggs).

Variation Sexual dimorphism of body size is rather pronounced (tab. 3). Females show smaller heads and shorter shanks than males. The differences of head size of the holotype of *O. poilani* (fig. 4) to the other females should be imputed to poor condition of this specimen, as well as absence of supraorbital horn, a dermal structure which might easily be destroyed. In life, the pupil of specimen IEBR D 231 showed horizontally enlarged diamond-shape, thus confirming the horizontal shape of pupil mentioned in the original description of the genus.

Distribution China, Thailand, Vietnam. Species previously not cited from Thailand

Etymology The Greek term *microstoma* describes the small mouth, characteristic for the species of this genus.

Ophryophryne pachyproctus Kou, 1985

Ophryophryne pachyproctus Kou, 1985: 41. – *Type-specimen* holotype, by original designation, YL A.8311032, adult male (not examined). – *Type-locality* Zhushihe (alt. 1000 m), Mengla Xian (21°29'N, 101°33'E), Yunnan, China

Specimens examined China: Zhushihe (alt. 1000 m), Mengla Xian (21°29'N, 101°33'E), Yunnan: CIB A 8311038, male, paratype, Vietnam: Nghe An Province. MNHN 2000 9087, male.

Diagnosis Small-sized *Ophryophryne*, with relatively short shank, large tympanum, small head. Dorsal coloration dark. Supraorbital horn small, anus terminal on a distinct dermal protuberance.

Description of paratype CIB A 8311038 (fig. 5) (A) Size and general aspect – (1) Specimen of rather small size (SVL 30.0 mm), body rather slender.

Table 3. – Measurements (mm) and per mille of snout-vent length (in parenthesis) of specimens of *Ophryophryne microstoma* Boulenger, 1903, including lectotype of *Ophryophryne microstoma* and holotype of *Ophryophryne poilani* Bourret, 1937. Means and standard deviations are given between square brackets.

Collection number	BMNH 1947.2.22.52	MNHN 1997.5258, 1997.5260; FMNH 254251	MNHN 1948.01.3	BMNH 1947.2.22.50-51, 1947.2.22.53, 1974.2334, 1997.5259, FMNH 254250
Locality	Mau Son, Vietnam	Ben En & Tam Dao, Vietnam	Dong-Tam-Ve, Vietnam	Ben En, Mau Son & Tam Dao, Vietnam
Status	Lectotype of *O. microstoma*	Additional material	Holotype of *O. poilani*	Paralectotypes of *O. microstoma* (BMNH) and additional material (FMNH)
Sex	Adult male	3 adult males	Adult female	6 females
Snout-vent length	39.1	38.1-44.4 [41.4 ± 3.17]	47.1	24.6-56.5 [46.1 ± 11.5]
Head width	9.5 (243)	9.7-12.4 (255-265) [11.1 ± 1.44 (273 ± 16.0)]	11.5 (244)	8.1-15.1 (242-329) [12.1 ± 2.47 (269 ± 33.0)]
Head length	9.4 (240)	9.0-11.9 (236-270) [10.7 ± 1.53 (258 ± 19.1)]	9.5 (202)	7.4-14.0 (236-401) [1.5 ± 2.59 (257 ± 26.8)]
Tympanum diameter	2.44 (62)	2.59-3.37 (68-78) [3.07 ± 0.42 (74 ± 5.07)]	2.72 (58)	1.52-4.60 (59-81) [3.09 ± 1.13 (66 ± 8.7)]
Thigh	15.8 (404)	19.0-19.6 (428-469) [19.3 ± 0.42 (44× ± 29.0)]	,9.8 (420)	11.5-25.2 (382-467) [19.6 ± 5.79 (414 ± 36.4)]
Shank	6.0 (419)	6.2-19.4 (423-464) [18.1 + 1.70 (438 ± 23.0)]	19.4 (412)	11.4-23.9 (372-463) [.8.9 ± 4.17 (414 ± 31.5)]
Foot	5.4 (394)	4.0-19.2 (367-438) [17.2 ± 2.78 (413 ± 39.2)]	18.6 (395)	9.6-20.8 (368-390) [17.2 ± 4.58 (378 ± 9.46)]

OHLER

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Fig. 4. – *Opisthothylax microstoma* Boulenger, 1903, MNHN 1948.0113, holotype of *Opisthothylax polaris* Bourret, 1937, adult female, SVL 43.1 mm. Dorsal view (top), lateral view of head (bottom).

Fig 5 *Ophryophyne pachyproctus* Kou, 1985 CIB A 8311038 paratype subadult male, SVL 30 0 mm
Dorsal view (top), lateral view of head (bottom)

(B) Head. (2) Head very small, slightly wider (HW 7.9 mm) than long (HL 7.4 mm, MN 6.5 mm, MFE 5.3 mm; MBE 2.7 mm), flat. (3) Snout truncate, very protruding, its length (SL 2.9 mm) shorter than horizontal diameter of eye (EL 3.4 mm). (4) Canthus rostralis sharp, loreal region concave, acute in cross section. (5) Interorbital space flat, narrower (IUE 1.5 mm) than upper eyelid (UEW 2.2 mm) and internarial distance (IN 2.4 mm); distance between front of eyes (IFE 4.4 mm) two third of distance between back of eyes (IBE 6.7 mm). (6) Nostrils rounded, without flap of skin laterally, at equal distance from eye (EN 1.0 mm) and tip of snout (NS 1.0 mm). (7) Pupil indistinct diamond. (8) Tympanum (TYD 2.2 mm) very distinct, rounded; smaller than half diameter of eye, tympanum-eye distance (TYE 1.2 mm) half its diameter (9) Pineal ocellus absent. (10) Vomerine ridge absent (11) Tongue rounded, not emarginate. (12) Supratympanic fold distinct, present from eye to above shoulder, posterior part enlarged

(C) Forelimbs. (13) Arm rather long, thin, fore-arm (FLL 7.5 mm) shorter than hand (HAL 7.9 mm), not enlarged. (14) Fingers long and thin; finger III long, thin (TFL *nm*) (15) Relative length of fingers, shortest to longest: I < II < IV < III. (16) Tips of fingers rounded, slightly enlarged. (17) Fingers without dermal fringe; webbing absent. (18) Subarticular tubercles indistinct, all absent. (19) Prepollex oval, distinct, a single, oval palmar tubercle; supernumerary tubercles absent.

(D) Hindlimbs. (20) Shanks four times longer (TL 13.1 mm) than wide (TW 3.4 mm), a little shorter than thigh (FL 14.3 mm), but longer than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 12.6 mm). (21) Toe IV long (FTL *nm*; TFOL 19.4 mm). (22) Relative length of toes, shortest to longest: I < II < V < III < IV (23) Tips of toes rounded, scarcely enlarged; discs absent. (24) Webbing absent (MTTF 6.1 mm, MTFF 6.2 mm; FTTF 7.1 mm; FFTF 6.50 mm). (25) Dermal fringe along toe V absent (26) Subarticular tubercles absent. (27) Inner metatarsal tubercle long, scarcely distinct, its length (IMT 1.3 mm) 1.77 times in length of toe I (TTL 2.3 mm) (28) Tarsal fold absent. (29) Outer metatarsal tubercle, supernumerary tubercles and tarsal tubercle absent.

(E) Skin. (30) Dorsal and lateral parts of head and body snout, between eyes and side of head shagreened; back shagreened with fine glandular folds and few glandular warts posteriorly, flanks with few glandular warts (31) Cephalic ridges absent. (32) Latero-dorsal folds, lateral line system and "Fejervaryan" line absent (33) Dorsal parts of limbs forelimb, thigh, leg and tarsus shagreened. (34) Ventral parts of head, body and limbs throat, chest, belly and thigh smooth (35) Femoral and pectoral glands small, present; supra-anal protuberance distinct, bearing at its distal part a ventral cloacal opening

(F) Coloration in alcohol. (36) Dorsal and lateral parts of head and body dorsal parts of head and dorsum almost uniformly dark brown, flanks slightly clearer, their lower parts clear greyish brown with few dark spots, more or less in a line; loreal region dark brown, tympanum orange brown, tympanic region dark brown, upper lip dark brown with an indistinct darker band (37) Dorsal parts of limbs dorsal part of forelimbs, of thigh, of shank and of foot brown with fine dark brown transversal bands, posterior part of thigh light greyish brown with a large dark triangular perianal zone extending to knees (38) Ventral parts of head, body and limbs throat brown, margin of throat dark brown, chest and upper part of belly brown, lower part yellowish with dark brown flecks; thigh yellowish, macroglands whitish

Table 4   Measurements (mm) and per mi,le of snout vent length (parenthesis) of two specimens, including paratype, of *Ophryophryne pachyproctus* Kou, 1985

Collection number	CIB A 8311038	MNHN 2000 9087
Locality	Zhushihe, China	Nghe An, Vietnam
Status	Paratype	Additional material
Sex	Subadult male	Adult male
Snout-vent length	30.0	28 9
Head width	7 9 (263)	8.3 (287)
Head length	7.4 (247)	8.3 (287)
Tympanum diameter	2 2 (73)	2 59 (90)
Thigh	14 3 (478)	11 7 (405)
Shank	13 1 (437)	12.0 (415)
Foot	12 6 (420)	12 1 (419)

Coloration in life (according to the original description).   Dorsal surface grey white or brown grey, a dark, distinct or indistinct triangle between eyes; side of head, lips, throat, chest and belly dark colored, sides of head and body bearing 4-6 black spots, posterior part of thighs and ventral surface of hands black brown, fore and hind legs dark colored, forearm and thigh generally with a large black spot; dorsal surface of hands and external surface of legs usually with black spots, palm and upper surface of hands orange red, tips of fingers light red, tips of toes dark. When put to alcohol, coloration gets darker, reddish parts turn white.

(G) Male secondary sexual characters. - Not observed (male not adult?).

Female sexual characters.   Not observed.

Variation - The measurements of the two specimens studied are given in tab. 4. Only larger samples might inform about the significance of the differences observed between the specimen from Vietnam and from China.

Distribution.   China (Yunnan) and Vietnam (Nghe An Province).

Etymology   The term *pachyproctus*, "having a thick vent", is derived from the Greek *pakhus*, "thick" and *proktos*, "vent".

KEY TO THE KNOWN SPECIES OF THE GENUS *Ophryophryne*

1a. Palmar tubercle distinct 2
1b Palmar tubercle indistinct   3
2a. Dorsal skin with glandular warts and horny spinules; cloacal appendage absent, adult males SVL 35 5-43 0 mm, TL 18.4-19.0 mm, adult female SVL 53 5 mm, TL 25.6 mm .... *O. hansi*
2b Dorsal skin shagreened, cloacal appendage present; adult males SVL 28.9-30 0 mm, TL 12 0-13.0 mm .... *O. pachyproctus*

3a. Dorsum dark brown, posterior part of shank with fine brownish marbling, body size small: adult males SVL 32.0-34.8 mm, TL 15.4-15 5 mm; adult females SVL 41 4-45 8 mm, TL 17.4-18.0 mm; vocal sacs absent .... *O. gerti*

3b. Dorsum greyish-brown; posterior part of shank with large brown spots; body size large adult males 38 1-44.4 mm, TL 16.0-19.4 mm; adult females SVL 46.3-56.5 mm, TL 18.1-23.9 mm; vocal sacs present ....*O. microstoma*

DISCUSSION

In *Ophryophryne*, several trends, which can also be observed in the sister-group *Xenophrys*, occur, such as diminutive size, reduction of palpebral horn and variation of structure in dorsal skin Characters used to differentiate these two taxa are mostly linked to reduction of the size of the skull in *Ophryophryne*.

The geographic distribution of the genus *Ophryophryne* includes Laos, Thailand, Vietnam (northern and central), as well as China (Yunnan and Guangdong Provinces) (fig. 6). It is completely included in the distributional range of its sister-group *Xenophrys*, but shows a much reduced extension. This range may still be increased by further observations, when field data are accumulated, as all over its range only few specimens have been collected since its description a century ago.

The species referred to the genus show a complex pattern of distribution The range of *O. pachyproctus* seems to be similar to that of *O microstoma*, as are the ranges of *O hansi* and *O. gerti*. The distribution areas of both species couples are allopatric with a large area without data The new species *O hansi* is known only from its type-locality. However, additional field data are likely to extend its range, as has occurred for *O pachyproctus*, which was known for some years from its type-locality only, but now can be considered as a member of the fauna of northern Vietnam. For *O microstoma* the distributional range can be extended to Thailand. There is no evidence for syntopic occurrence of two or more species of *Ophryophryne O gerti* and *O. hansi* have the same collecting locality, but the females of *O. gerti* were collected in a swampy area, whereas *O hansi* males were actively calling along a stream (INGER et al , 1999). This does not confirm that the two species occur in different habitats, as obviously one species was reproductively active, but not the other. Mature *O microstoma* were collected along a small stream (personal observation), as was described for *O hansi O microstoma* and *O pachyproctus* share a large distribution range On the opposite, *O pachyproctus* and *O gerti* do not share distribution range according to the current data.

The synonymy of *O poilani* is based on morphological data, especially on measurement of tibia length, which should be relatively precise despite the poor state of preservation of its type-specimen *O hansi* is the species showing the largest head size, but the type of *O poilani* has a head width smaller than all studied specimens of *O hansi* The type-specimen of *O poilani* clearly is not conspecific with the specimens that INGER et al (1999) mentioned as *O poilani* This type specimen has definitely shorter tibia than *O hansi*, but its tibia length is included in the range of variation observed in *O microstoma*.
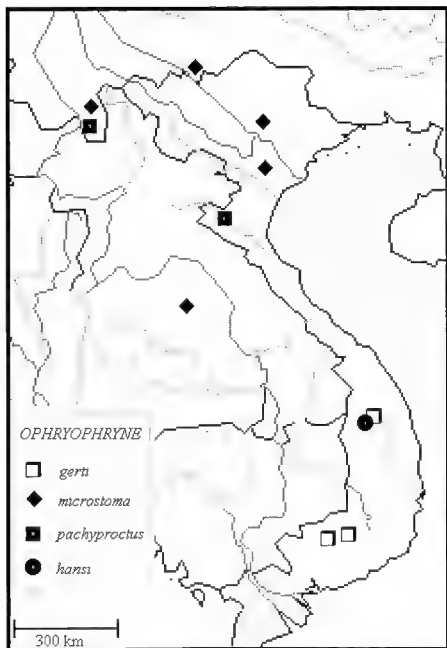
Fig. 6 – Collection localities of species of the genus *Ophryophryne* Boulenger, 1903

Ophryophryne hansi is relatively distinct from the other three species and shows plesio-morphic characters, such as relatively large head (320 p.m. of SVL) and large body size. The cloacal appendage of *O. pachyproctus* is a unique character, present only in this species. The tubercles on the vent observed in some of the specimens of other species of *Ophryophryne* do not form a cone including the anal opening. They form dermal structures which surround the anal opening. Size reduction is probably independent in *O. pachyproctus* and *O. gerti* as both only share this character. The two species are distinct for presence of palmar tubercles, length of inner toe and size of tympanum.

Ophryophryne species show an important reduction of head size. These species have a small mouth and a tongue fixed to the mouth floor which does not allow them to capture and swallow large-sized prey. Such morphological adaptations can be observed in various groups of frogs and has been studied in *Rhinophrynus* Duméril and Bibron, 1841 and in the Microhylidae Noble, 1931 (TRUEB & GANS, 1983; BLUM & MENZIES, 1988). A small head is usually linked to a special nutritional mode and a fossorial life (DUELLMAN & TRUEB, 1985). The shape of the hindlimbs, in particular the feeble development of the inner metatarsal tubercle, does not indicate any particular adaptation to fossorial life in *Ophryophryne*. The particular buccal anatomy might be linked to the nutritional mode of these species. Their digestive tract is well developed, showing a large gastric pouch, but it was found empty in the specimens examined (personal observations). Nothing is known about foraging in nature. In laboratory conditions they accept young insects as well as earthworms (R. Boistel, unpub-lished observations). The structural similarity of buccal anatomy in *Ophryophryne* and *Xenobatrachus* and *Xenorhina* (Microhylidae) might indicate that these frogs have similar diets. *Xenobatrachus* and *Xenorhina* feed on earthworms (BLUM & MENZIES, 1988) and have well developed vomerine teeth on the buccal roof, which seem to be crucial for ingestion of this food. Such structures are absent in *Ophryophryne*. New data on the biology of these species will be necessary to understand the ecological role and niche of small mouthed megophryids in the amphibian communities of southeast Asian primary forests.

RÉSUMÉ

L'étude des spécimens-types et des spécimens recemment collectés de crapauds du genre oriental *Ophryophryne* Boulenger, 1903 (Megophryidae) nous mène à la redéfinition des taxa reconnus et de la définition de deux nouvelles especes dont une est rapportée du Vietnam et du Laos et l'autre seulement du Vietnam. *Ophryophryne poilani* Bourret, 1937 est mis en synonymie d'*Ophryophryne microstoma* Boulenger, 1903. L'aire de distribution de l'espece *O. microstoma*, qui incluait le Vietnam et la Chine, est élargie à la Thaïlande. *Ophryophryne pachyproctus* Kou, 1985 est confirmé du Vietnam.

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A redescription of the external
and buccopharyngeal morphology
of the tadpole
of *Ophryophryne microstoma*
Boulenger, 1903 (Megophryidae)

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**The external morphology and the buccopharyngeal features of the
tadpole of *Ophryophryne microstoma* Boulenger, 1903 are redescribed.
Morphometric data are provided. Few morphological deviations as compa-
red to the previously described tadpoles from China are noted. The
taxonomic status of the genus *Ophryophryne* within the Megophryidae is
discussed in the light of the tadpole morphology.**

INTRODUCTION

Ophryophryne Boulenger, 1903 is a small group of species from southeast Asia with a
rather limited distribution, still little studied, and including now four species after a recent
taxonomic revision of the genus (OHLER, 2003). The status of *Ophryophryne* has always been
confused Though its descriptor noticed its overall resemblance with members of the Peloba-
tidae (BOULENGER, 1903a), he included this genus within the Bufonidae (BOULENGER, 1903b)
and it is still yet considered as such by some authors (NGUYEN & HO, 1996). It was then put
within the Pelobatidae by NOBLE (1926) The status of the taxon *Ophryophryne* among the
Megophryidae has already been discussed in previous works (NOBLE, 1926, DUBOIS, 1980,
1987; RAO & YANG, 1997; DUBOIS & OHLER, 1998) RAO & YANG (1997) rose *Ophryophryne*,
Atympanophrys Tian & Hu, 1983, *Brachytarsophrys* Tian & Hu, 1983, *Megophrys* Kuhl & Van
Hasselt, 1822 and *Xenophrys* Günther, 1864 to the generic level on the basis of cytological,
morphological and ecological characters. DUBOIS (1980) put first *Ophryophryne* within the
genus *Megophrys* then on the basis of new subdivisions within the genus *Megophrys* a str
re-evaluated his proposition and gave *Ophryophryne* a generic status (DUBOIS, 1987) Though
its position seems now to be clearly within the Megophryidae and the genus *Xenophrys* has

been identified as its sister-group by several authors (TIAN et al., 1985; RAO & YANG, 1997), its generic or subgeneric status (within the genus *Megophrys*) is still discussed (MATSUI in FROST, 1985; YE et al., 1993; MANTHEY & GROSSMANN, 1997)

Ophryophryne adults bear autapomorphies, which distinguish them from other members of *Megophrys* (sensu lato including four subgenera, i.e., *Atympanophrys*, *Brachytarsophrys*, *Megophrys*, *Xenophrys*). absence of maxillar and vomerine teeth and presence of a horizontal pupil. However, are these characters sufficient to consider *Ophryophryne* as a valid genus? Anuran tadpoles are, as a general rule, well intergenerically differentiated on the basis of the buccopharyngeal morphology (VIERTEL, 1982, Grosjean, unpublished data) The aim of this work is, besides a description of the morphology and buccopharyngeal features of the only known tadpole of the genus, to compare these data with those of known tadpoles of the four subgenera of the genus *Megophrys*, in order to discuss the status of *Ophryophryne* in the light of larval data.

MATERIALS AND METHODS

A total of 52 tadpoles, all *Ophryophryne microstoma* Boulenger, 1903, were collected in Ben En National Park, Thanh Hoa Province, Vietnam (19°30'-40'N, 105°21'-35'E) during August 1997. This national park is situated in a region of low hills surrounding the Song Muc Lake. Altitude ranges from 20 to 497 m above sea level, with most areas being below 200 m. The vegetation is that of a tropical semi-evergreen forest partly degraded by human activity. The climate is subtropical, with the heaviest rainfall between July and October The average temperatures between 1961 and 1990, in the months of July and August, were 28 9 and 27 8°C respectively (TORDOFF et al., 1997).

Some tadpoles were preserved soon after capture whereas others were reared in bowls of 24 cm of average diameter and 10 cm depth, and were fed with baby fish food (TetraMin). Tadpoles in developmental stages 25-43 (GOSNER, 1960) were preserved in a mixture of equal parts of 4 % formaldehyde and 70 % ethanol (GRILLITSCH, 1984). Some tadpoles reached metamorphosis assuring the identity of the species and were preserved in the same solution. This material is deposited in the collections of the Muséum national d'Histoire naturelle de Paris (MNHN 1999.0521-0572).

Morphological terminology follows ALTIG & MC DIARMID (1999), developmental stages were determined according to GOSNER (1960) and terminology of buccopharyngeal features follows WASSERSUG (1976). Measurements were taken with a graduated ocular attached to a stereomicroscope except for the total length and the distance from opening of vent to tip of tail which were measured with a hand caliper The distance from tip of snout to nares was not taken into account because the tip of snout was hidden beneath the oral funnel For exact location of measurement landmarks, see GROSJEAN (2001 fig. 2), except for tip of snout which is taken from the point where the funnel originates with the head anteroventrally. Drawings were made with the aid of a camera lucida

Preparation for SEM examination (JEOL JSM 840) comprised dehydratation (ethanol), critical-point-drying (liquid carbondioxide) and gold sputter surface coating.

RESULTS

ECOLOGICAL CONSIDERATIONS

The tadpoles studied were collected along a little stream running in the forest. The stream was 1-2 m wide and its depth ranged from a few centimetres in fast-flowing parts to up to 70 cm in the deepest pools. The bottom was mainly made up of rocks and stones, and of sand covered by dead leaves in the quiet pools. These tadpoles belong to the lotic-neustonic ecomorphological guild of ALTIG & JOHNSTON (1989). They were found in the lower part of the stream where the cover of vegetation was more open, in shallow water, hidden between the stones with their funnel open at the interface air-water. Tadpoles were also found near the banks of the stream, where the water ran between the stones, the tadpoles not being visible (as already noticed for tadpoles of the genus *Megophrys* by HORA, 1928) and in a little natural dam made up by branches and dead leaves. All developmental stages (from stage 25 to imago) were found all together at the same time and in the same part of the stream. This suggests that the mating and/or spawning period might be prolonged (parsimonious assumption) or that larval development is very slow and extends all over the year rather than being limited to a circumscribed period (in accordance with other observations). Indeed the tadpoles reared for one month did not show evolution (except for the latest stages). Slow development is not rare among Megophryidae and was observed in other genera like *Leptobrachium* Tschudi, 1838, *Leptolalax* Dubois, 1980, *Scutiger* Theobald, 1868 and *Oreolalax* Myers & Leviton, 1962 (SMITH, 1917; LIU & HU, 1960, CHEN et al., 1984, ZHAO et al., 1994; pers. obs.) and in rheophilous species in general. Few tadpoles of *Leptolalax* sp. were found among them. Numerous tadpoles of *Leptobrachium chapaense* (Bourret, 1937) lived in the pools of the same stream but not in the same niche (no tadpole of *Ophryophryne microstoma* was found in pools). Clutches of *Rana (Sylvirana) nigrovittata* (Blyth, 1855) were found in crab holes, in the bank.

During the two months spent in the field, the reproduction of the species which produced the tadpoles was not observed: advertisement calls were not heard and neither mates in amplexus nor egg clutches were found. Non-calling adults of *O. microstoma* were occasionally found among the vegetation of the bank and on emerged rocks in the stream bed.

DESCRIPTION OF TADPOLE

External morphology

Gross morphometric parameters (SVL and TL) of all tadpoles are presented in table 1. The following description is based on four tadpoles at stages 35-38 (MNHN 1999 0532-0535), except where specified. Detailed morphometric data are presented in table 2. In dorsal view (fig. 1a), body elliptical. Eyes of moderate size (diameter about 0.1 time body length), bulging, separated by a distance which equals about 1.3 times the internarial distance, directed and positioned laterally, visible in ventral view. Nares tubular, of moderate size, directed laterally

Table 1   Variation of snout-vent length (SVL) and total length (TL) with stage (GOSNER,
1960) in tadpoles of *Ophryophryne microstoma*. Number of tadpoles (*n*) examined,
mean value ± standard deviation in mm (range in parentheses).

Stage	*n*	SVL	TL
25	24	5.87 ± 0.74 (5.06-8 55)	17.49 ± 2.19 (15.00-24.30)
26	7	7.83 ± 0.50 (7.06-8 55)	22.75 ± 1.34 (20.65-24.75)
27	2	8.62 ± 0.28 (8.42-8.82)	26.35 ± 0.07 (26.30-26.40)
28	2	9.14 ± 1.21 (8.29-10.00)	27.45 ± 2.05 (26.00-28.90)
31	3	9.56 ± 0.20 (9.34-9.74)	27.28 ± 0.88 (26.35-28.10)
34	1	10 92	31.05
35	1	9 47	28.10
37	2	10.66 ± 0.00 (10 66-10.66)	30.70 ± 3.54 (28.20-33.20)
38	1	10 66	32.40
40	1	11 18	31.60
41	5	9.87 ± 0.57 (9.21-10.53)	28.42 ± 1.54 (25.85-29.65)
42	1	10 26	29.75
43	1	11.18	25.55

Table 2 – Morphometric data for tadpoles of *Ophryophryne microstoma* in avanced
developmental stages (35-38, GOSNER, 1960) BH, maximum body height, BW,
maximum body width, ED, maximum eye diameter, HT, maximum tail height, LF,
maximum height of lower tail fin, MNHN, collection number, Muséum national
d'Histoire naturelle, Paris, *nm*, no measurement; NN, internarial distance, NP, naro-
pupillar distance; PP, interpupillar distance; SS, distance from tip of snout to opening of
spiracle; SU, distance from tip of snout to insertion of upper tail fin; SVL, snout-vent
length; TL, total length, UF maximum height of upper tail fin; VT, distance from vent
opening to tip of tail.

Stage	MNHN	SVL	TL	SS	SU	VT	HT	UF
35	1999.0535	9.47	28.10	4.21	11.71	19.30	4 99	1 28
37	1999.0534	10 66	28.20	4.67	10.79	18 60	4 86	1 24
37	1999.0533	10 66	33.20	4.44	14.34	21.50	4.86	1.31
38	1999.0532	10 66	32.40	4.93	8 03	21.70	4 99	1 34

Stage	MNHN	LF	BH	BW	ED	PP	NN	NP
35	1999.0535	1.40	*nm*	*nm*	1 01	3.24	2 61	0 75
37	1999.0534	1.18	4 15	4.73	1 09	3.50	2.72	0 93
37	1999 0533	1.18	4.15	4.73	1 09	3.64	2.71	0 93
38	1999 0532	1.24	4.08	4.99	1 10	3 48	2 49	0 96

and horizontally, and positioned rather dorsally, closer to pupils than to tip of snout. In profile (fig. 1b), body depressed. Spiracle sinistral, conical, very short, attached to the body wall except its tip which is free, positioned just beneath the longitudinal axis, oriented posteriorly. Spiracular opening situated slightly closer to pupil than to the end of the body, and at a level situated just beneath the apex of the caudal myotomes (fig. 1b) to beneath the apex of caudal myotomes and the hindlimbs, its opening from rounded to oval. Tail musculature strong, gradually tapering, almost reaching tail tip (very near to the end). Tail fins shallow, moderately developed, not extending onto body, dorsal fin slightly higher than ventral fin in the distal half of the tail; free margin of dorsal fin horizontal and very shallow in the proximal half of the tail then following tail musculature; free margin of ventral fin parallel to tail musculature. Point of maximum height of tail located just before halfway of the tail, in the proximal part, tail tip bluntly pointed. Vent tube of moderate size, medial, tubular (often slightly bulging in the middle), directed posteriorly, not linked to ventral tail fin, opening medial. Neither skin glands nor neuromasts visible.

Oral disk subterminal (fig. 2), lips expanded vertically forming a dorsally oriented funnel; lateral corners pronounced; upper lip smaller than lower; lips lacking keratodonts, but furnished with a few short, low ridges (variable number among specimens), more densely arranged on the upper labium than on the lower one: arrayed in 20 longitudinal rows (in mean) and 2 (on the upper labium) to 4 (on the lower labium) transversal rows (without clear limits), no marginal papillae. Width of expanded funnel about 50 % of body length (35 % when folded, which is often the case in the preserved specimens) At stage 40 the funnel began to be resorbed, at stage 42 the posterior part of the funnel disappeared while the anterior part still persisted. At stage 43 the funnel entirely disappeared. Lower jaw sheath (fig. 3a) straight anteriorly, radically curved backward laterally, entirely white, its free margin bearing fine, pointed, hair-like serrations; upper jaw sheath (fig. 3b) nearly straight, notched medially, bearing fine and elongate serrations only in the medial third of its free margin, brown grey with a white margin; both beaks soft.

Colour in preservative

Dorsal side of body and upper part of flanks brownish-khaki. Lower part of flanks weakly mottled with the same colour; ventral side of head (from snout to posterior part of eyes) intensely coloured. Belly white, intestine not visible through body wall. Caudal muscle weakly coloured (more on upper than on lower portion, with emphasis on the myotome apexes), tail fins translucent with few spots (more on upper than on lower fin); half to a quarter of distal part of tail often intensively coloured in dark brown. Oral funnel greyish with brownish-khaki papillae. There is considerable intrapopulational variation in colour: certain individuals are almost unpigmented whereas others are strongly coloured, others have a tail strongly coloured except in the distal quarter.

Tadpole at stage 45 (just metamorphosed, MNHN 1999 0524, SVL 11 97 mm) in preservative. Head and dorsum brown, flanks and dorsal part of thigh and tibia with large white tubercles. Dorsal folds present. Supratympanic fold underlined with white above and black below; the black line extending as far as the armpit. Limbs white below, faintly tinted with brown above. The above features began to appear from stage 42 on.
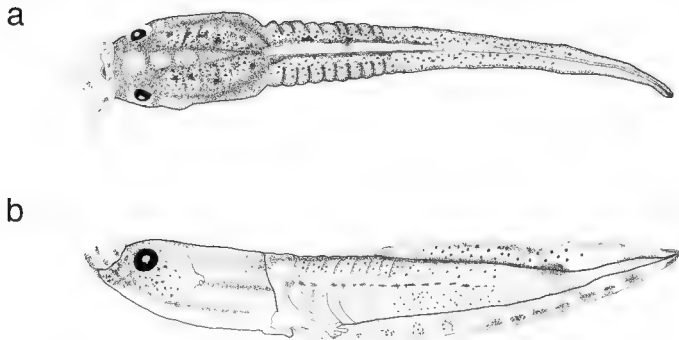
Fig 1 *Ophryophryne microstoma* (stage 38, TL 32,1 mm, MNHN 1999.0532) a, dorsal view; b, lateral view.
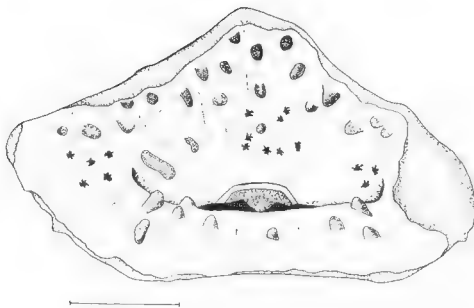
Fig 2 Funnel-like mouth of *Ophryophryne microstoma* (stage 38, MNHN 1999 0532) Scale line 1 mm

Internal buccal features

The description is based on a single tadpole at stage 37 (MNHN 1999.0534).

Buccal floor (fig. 4a), a soft lower jaw sheath present at entry of buccal cavity, straight anteriorly, radically curved backward laterally, a nodule on the inner wall of the beak at the level of curvatures. Prelingual arena deep, with two successive pairs of palps directed medially, followed by a fifth palp in median position. These structures are thick, fleshy and smooth lobes, concave anteriorly, the first pair reaching almost the lower jaw sheath being visible without dissection. Tongue anlage distinct, not very prominent, drop-shaped, position-ed on an elevated mass, lingual papillae absent. Buccal floor arena forming an elongate oval, in a depression, without buccal floor arena papillae but its anterior half bounded laterally by a thick ridge on each side, these two ridges merging with the elevated part bearing the tongue anlage anteriorly. The ridges ending posteriorly in front of the buccal pockets with elevated knobs each wrapped by an anteriorly concave flap, posterior half of arena bounded by an undulating ridge on each side. Anterior part of arena with a median groove of about a third of the length of the buccal floor arena, 2-5 pustules on each side between the ridges and the median groove, posterior part of arena lacking ornamentations. Buccal pockets short, transversely oriented, arched anteriorly, with fine openings, area anterior to buccal pockets with 1-3 pustules on each side, area posterior to buccal pockets with less than 10 small
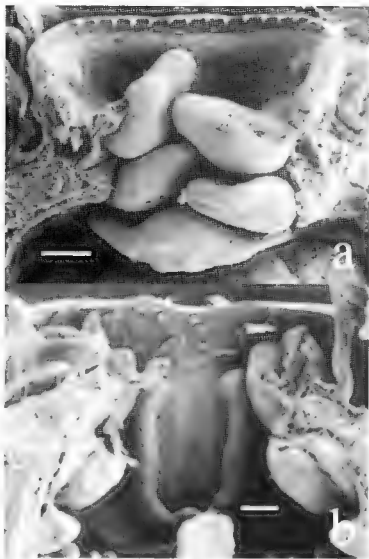
Fig. 3 Close-up view of the jaw sheaths of *Ophryophryne microstoma* (stage 37, MNHN 1999 0534) a, lower part; b, upper part. Scale line: 0.1 mm

papillae. Ventral velum slightly undulated, its medial part extending backward; two minor projections laterally, medial notch absent; spicular supports present laterally, secretory pits of ventral velum absent, glottis slightly exposed. Branchial baskets large; a single common filter cavity on each side, filter rows wide with tertiary or higher-order ramifications, mesh size about 100 μm

Fig 4   *Ophiophrene microstoma* (stage 37 MNHN 1999 0534) a buccal floor arena b. buccal roof arena

Buccal roof (fig. 4b) upper jaw sheath nearly straight, bearing fine and elongate serrations only in the medial third. Prenarial arena wide, trapezoidal, in medial position a large U-shaped ridge with a posteromedial knob, its anterior arms almost reaching the neck; a little knob just posterior to the U-shaped ridge (hidden by the median ridge), on the wall of the prenarial arena two pairs of well pronounced dorsoventrally compressed ridges aligned longitudinally. Choanae transverse, short; anterior narial wall smooth, with a short, stocky papilla on the internal end and another even stockier on the external end, narial valve smooth with a small stocky triangular projection located rather medially. Postnarial arena bounded laterally by a pair of pronounced ridges (which could be the homologue of postnarial papillae), fused anteriorly with the medial posterior wall of choanae, ending behind the medial ridge, their posterior ends curved medially. Median ridge a tall straight projection directed anteriorly plus three little prominent lobes, reaching as far as the posteromedial knob of the prenarial U-shaped ridge. Postnarial arena filled by the body of the median ridge. Lateral ridge papillae a large dorsoventrally compressed flap; above their anterior part a similar but smaller flap. Buccal roof arena with about fifty pustules arranged more densely posteriorly, no buccal roof arena papillae but two large nodules fused on each side bounding anterolaterally the buccal roof arena and abutting the ridges lateral to the medial ridge. About ten pustules on each lateral wall of the buccal roof, at the level of the anterior half of the buccal roof arena. Posterolateral ridges present but not very prominent laterally and medially, and rather distinct lateromedially. Glandular zone rather indistinct, absent medially; secretory pits absent. Dorsal velum curved ventrally, interrupted medially

DISCUSSION

Among the four species in the genus *Ophryophryne* known at present, only the tadpole of *O. microstoma* has been described previously. I redescribe here the tadpole of the species based on specimens belonging to a much more southern population.

LIU & HU (1962) reported on the external morphology of the tadpole from Kwangsi Province, China. These authors did not specify the developmental stage of the tadpole upon which their description was based but just noticed that it bore buds of hind limbs and had a total length of 33 mm. The only tadpole in our sample which reached this size was a tadpole of stage 37. Hence, tadpoles in equivalent developmental stages were larger in the Chinese sample than in the Vietnamese sample. The other characters differing between the two samples were: oral disk bigger, eyes larger and tip of tail rounded (not bluntly pointed as in this sample) in the Chinese population. Differences were also observed in the number of papillae of the funnel: 15 longitudinal rows and three transversal rows in the Chinese population, 20 longitudinal rows (in mean) and 2-4 transversal rows (without clear limits) in our sample. Finally, the coloration varied in a few points: in the tadpole of the Vietnamese population the upper fin was rimmed with dark margins in its anterior part and the anterior part of the lower fin was coloured with large dark marks whereas it was white in the Chinese one. The imago collected by LIU & HU (1962) was comparatively large (14 mm body length and 3.5 mm tail), whereas an imago entirely metamorphosed collected in the Vietnamese population was about 12 mm in length). However in both cases the adult characters appeared

early since the skin folds and the tubercles were present before resorption of tail The eyelid processes seemed to appear after total resorption of tail.

The buccopharyngeal features of a specimen from Longjin, Guangxi Province, China were reported by HUANG et al. (1991). Their illustration showed some differences with our data In the buccal floor of the HUANG et al. (1991) specimen the posterior pair of palps as well as the single medial palp are shorter than in our specimen and a medial notch is present. Within the buccal roof, our specimen had a bigger prenarial ridge, two papillae on anterior narial wall and another on the narial valve whereas only one was present on the anterior narial wall in the Longjin specimen; moreover, pustulations in the buccal roof arena were present in the Vietnamese tadpole

The tadpoles of the genus *Megophrys* sensu lato (including the subgenera *Atympanophrys*, *Brachytarsophrys*, *Megophrys* and *Xenophrys*) have been little studied and their detailed descriptions are rare: (1) for the external morphology, *M. (X.) aceras* (Boulenger, 1903) (LAIDLAW, 1900, ANNANDALE, 1912, 1917, SMITH, 1926 [all under the name *M montana*]), *M. (X.) major* (Boulenger, 1908) (ANNANDALE, 1912), *M. (X., parva* (Boulenger, 1893) (ANNANDALE, 1912), *M. (X.) boettgeri* (Boulenger, 1899) (ANNANDALE, 1917; POPE, 1931; LIU, 1940), *M. (X.) longipes* (Boulenger, 1885) (LEONG & CHOU, 1998), *M. (X.) minor* Stejneger, 1926 (LIU, 1950), *M. (M.) montana* Kuhl & Van Hasselt, 1822 (BOULENGER, 1908), *M. (M.) nasuta* (Schlegel, 1858) (INGER, 1985); (2) for the buccopharyngeal features, *M. (B.) carinensis* (Boulenger, 1899) (HUANG et al., 1991), *M. (X.) minor* (WASSERSUG, 1980; HUANG et al., 1991), *M. (M.) nasuta* (INGER, 1985), *M. (X.) omeimontis* Liu, 1950 (HUANG et al., 1991) and *M. (A.) shapingensis* Liu, 1950 (HUANG et al., 1991). The tadpoles of the genus *Megophrys* sensu lato are very similar to those of *Ophryophryne* and nothing allows to distinguish them externally. The most peculiar structure of these animals, the funnel-like oral disc surrounding the mouth, is very conservative and its typical morphology is encountered in all species. The small differences reported in terms of variation in number of rows or of ridges are not greater between *Ophryophryne* and *Megophrys* sensu lato than between the members of the genus *Megophrys* sensu lato themselves (Grosjean, unpublished data) Of all the species on which the width of the funnel was measured, the tadpole of *Ophryophryne microstoma* is the one which possesses the smallest [50 % of SVL vs. 74.4 % in *M minor* (LIU, 1950) and *M boettgeri* (LIU, 1940), and 82.3 % in *M. aceras* (LAIDLAW, 1900)]. LEONG & CHOU (1998) did not give a measurement comparable but noticed that the funnel of *M. longipes* is the largest of all the species known The tadpoles of these two genera bear another peculiar structure, unique among the Megophryidae: soft jaw sheaths with long serrations at the opening of the mouth (INGER, 1985; HUANG et al., 1991, this paper). This structure, although externally visible, is not always conspicuous. It is now largely accepted that buccopharyngeal features are very conservative within genus (e.g. VIERTEL, 1982) as, e.g., within the Megophryidae (INGER, 1983, for a taxonomic review of three genera with larval characters, HUANG et al., 1991). Each megophryid genus has a typical buccopharyngeal morphology, which distinguishes it clearly from all other megophryid genera However, in contradiction to HUANG et al (1991)'s conclusion (not detailed in their work), I failed to find any significant differences in their buccopharyngeal features. The morphology of these tadpoles does not contribute to clarify the status of *Ophryophryne*, but the lack of clear differences between *Ophryophryne* and the species of the four taxa included in *Megophrys* (sensu lato) does not justify a different taxonomical level for the former A recent study based on cytology, morphology and ecology

(RAO & YANG, 1997) suggested two clades within this group, one including large species (*Atympanophrys*, *Brachytarsophrys* and *Megophrys*), the other including small and moderate-sized species (*Ophryophryne* and *Xenophrys*). Furthermore, RAO & YANG (1997) proposed that these five taxa should be risen to generic level. The results of the present study do not conflict with the opinion of these authors.

RÉSUMÉ

La morphologie externe, incluant des données morphométriques et l'anatomie bucco-pharyngée du têtard d'*Ophryophryne microstoma* Boulenger, 1903 sont présentées. Les individus de cet échantillon présentent quelques differences morphologiques avec des têtards rapportés à cette espèce mais appartenant à d'autres populations. Le statut taxinomique du genre *Ophryophryne* au sein des Megophryidae est discuté à la lumière des caracteristiques morphologiques et buccopharyngées du têtard d'*Ophryophryne microstoma* et de celles du genre *Megophrys* au sens large publiés dans la littérature.

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Larval stages, habitat and distribution
of the hyperoliid frog
Heterixalus rutenbergi (Boettger, 1881)

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We describe the hitherto unknown external larval morphology of *Hete-
rixalus rutenbergi*, a reed frog from highlands in central Madagascar.
Tadpoles were collected in a sun-exposed pond in a swampy savannah at the
Itremo Massif. Their morphology is similar to that of other *Heterixalus*,
with a labial tooth row formula of $1/1+1:2$. They differ by a distinct marbled
or spotted color on the proximal third of the caudal musculature. Metamor-
phosing juveniles have the distinctive pattern of adult frogs with five white
stripes on a green dorsum, unlike other *Heterixalus* who show a juvenile
coloration with two dorsolateral stripes. Contrary to other *Heterixalus*
species, *H. rutenbergi* seems to be restricted to highland savannahs and
has so far not been recorded in high densities; its status should therefore be
more carefully monitored.

INTRODUCTION

The genus *Heterixalus* Laurent, 1944 contains the endemic Malagasy representatives of
the family Hyperoliidae. *Heterixalus* is the sister group of the Seychellean *Tachycnemis*
Fitzinger, 1843 in this otherwise exclusively African family (RICHARDS & MOORE, 1996,
VENCES et al., 2003). Currently 10-11 species of *Heterixalus* are known (VENCES et al., 2000),
two of which are endemic to the highlands of central and central-eastern Madagascar: *H.
betsileo* (Grandidier, 1872) and *H. rutenbergi* (Boettger, 1881).

Heterixalus species are typical inhabitants of open areas, and often occur in secondary
habitats such as rice fields. Their larvae are of a rather generalized pond type, with a single
uninterrupted row of labial teeth on the upper lip, and one interrupted and two uninterrupted
rows on the lower lip. This morphology has been ascertained by BLOMMERS-SCHLOSSER (1982)
and GLAW & VENCES (1993, 1994) for *H. betsileo*, *H. madagascariensis* (Duméril & Bibron,
1841), *H. boettgeri* (Mocquard, 1902) and *H. luteostriatus* (Andersson, 1910).

Heterixalus are also very uniform in adult morphology, and a reliable species distinction is only possible by combining advertisement calls and coloration in life (GLAW & VENCES, 1993). However, one species, *H. rutenbergi*, has a number of highly divergent traits: its call bears no resemblance to that of any other species, the gular gland on the vocal sac of males has blackish color, and the dorsal pattern (green with five longitudinal white bands) is unique. We recently started with intensive herpetological surveys in the montane areas of central Madagascar (see VENCES et al., 2002). During the fieldwork, we discovered tadpoles that could be unambiguously assigned to *H. rutenbergi* by the pattern of metamorphosing juveniles. In the present paper, we describe the morphology of these tadpoles and review the published information on distribution and habitat of *H. rutenbergi*.

MATERIALS AND METHODS

Tadpoles were collected on 11 March 2001 at Ambatomenaloha, Itremo Massif, central Madagascar (19°58'S, 46°55'E; 1820 m above sea level). They were found in a shallow sun-exposed pond on a large unforested plain that partially was flooded by a river. Most ponds on this plain were fed by the river and had relatively cold water, whereas the ponds populated by *Heterixalus* tadpoles were much warmer, but no measurements of temperature could be effectuated. The pond had a depth of ca. 60 cm, and was bordered by grass only. The specimens were preserved in 5‰ formalin after capture, but were damaged during the transport. A batch of 14 tadpoles were deposited in the herpetological collection of the Zoologische Staatssammlung München under the number ZSM 789.2001. One additional specimen (field number LR 271) used for the detailed morphological description and drawings will be incorporated in the ZSM later on. Developmental stages are described after GOSNER (1960). Morphological measurements were taken by L. R. using a digital caliper to the nearest 0.1 mm, following landmarks, terminology and definitions of McDIARMID & ALTIG (1999). The formula of labial tooth rows follows DUBOIS (1995).

We use the following abbreviations: BL, head and body length (in tadpoles: from the tip of the snout to the junction of the posterior body wall with the axis of the tail myotomes, McDIARMID & ALTIG 1999); TAL, tail length; BW, maximum body width; ODW, maximum width of oral disc; DGMP, dorsal gap of marginal papillae; IOD, interorbital distance between centers of pupils; ED, eye diameter; TH, tail height at beginning of tail; MTH, maximum tail height including the caudal fin; TMH, height of caudal musculature at mid-tail; TMW, caudal muscle width; SVL, snout-vent length (in adult and juvenile frogs); UTR, upper tooth row; LTR, lower tooth row.

RESULTS

The series of tadpoles assigned to *Heterixalus rutenbergi* had a conspicuous color pattern. They were brownish with green olive, and had a very distinct silvery white marbling on the proximal third of the caudal musculature (fig. 1a-b). In late developmental stages

(42-45) the typical adult coloration (green dorsum with five white longitudinal stripes, each bordered by two black lines) became visible (fig. 1c).

The following morphological description is based on one tadpole in stage 37 (field number LR 271, fig 2a-c). Tail only partly preserved, part of the skin detached. A rather compressed tadpole of ORTON's (1953) type 4; eyes directed laterally, spiracle sinistral and positioned closer to the anus than to the tip of snout; caudal fin, as far as recognizable, dorsally and ventrally with straight edges, starting directly behind body (fig 2b); intestine not visible through the ventral skin. Further proportions and detailed characters of body and tail not reliably assessable because of poor state of preservation.

Oral disc apparatus in excellent state of preservation (fig. 2c), generalized, small, almost terminal, oriented ventrally, labial tooth row formula 1/1+1:2; tooth rows distinct but relatively small; LTR1 with a small gap (< 0.1 mm); UTR1 with approximately 80 labial teeth (ca. 34 per mm). Oral disc without a recognizable lateral notch; beak distinct and black, both jaw sheaths with serrations at their cutting edges Oral papillae present around the oral disc except for its upper part, 1-2 rows of submarginal papillae, restricted to lateral parts of oral disc; marginal papillae in one row; underneath about 37 marginal and 8-10 submarginal papillae, all shorter than 1 mm.

Morphometric measurements. BL 14.4 mm; TAL (incomplete) 14 9 mm; BW 9 4 mm; ODW 1.7 mm; DGMP 1 7 mm; IOD 5 6 mm; ED 2.1 mm; TH 5.4 mm; MTH 8.8 mm; TMH 4.8 mm; TMW 3.5 mm; UTR1 1.9 mm; each part of LTR1 0 8 mm; LTR2 1.8 mm; LTR3 0 7 mm.

In preservative, anterior lateral surface of body dark brown with yellowish shade, posterior part dark brown with some larger silvery shades, whole dorsum dark brown with many black spots of 0.4-1.6 mm diameter (fig. 2a-b) Similar spots also on dorsal and ventral caudal fins, and on caudal musculature (0 6-2 3 mm in diameter) Belly white with many smaller black spots.

In a just metamorphosed juvenile (fig 1c), the color pattern typical for adult *H rutenbergi* was already fully expressed SVL of one specimen in stage 41-42 belonging to the series ZSM 789.2001 is 15.5 mm.

No adult *H rutenbergi* were found during our survey at Itremo. Other frog species collected or observed by us were *Boophis ankaratra* Andreone, 1993, *B goudoti* Tschudi, 1883, *B luteus* (Boulenger, 1882) (call record), *B microtympanum* (Boettger, 1881), *Mantidactylus* aff *brevipalmatus* Ahl, 1929, *M domerguei* (Guibé, 1974) (call record), *M femoralis* (Boulenger, 1882), *M lugubris* (Duméril, 1853), *M* sp. A. aff. *curtus* (Boulenger, 1882), *M* sp. B aff. *curtus* and *Ptychadena mascareniensis* (Duméril & Bibron, 1841) Furthermore, a collection made by D Rakotomalala included a subadult specimen of *Scaphiophryne madagascariensis* (Boulenger, 1882).
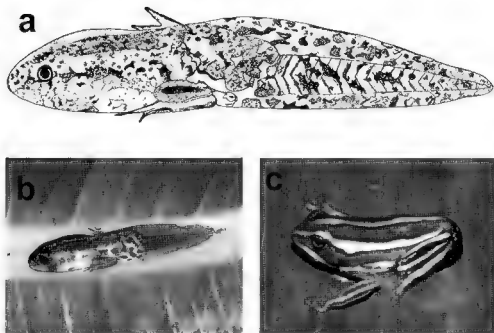
Fig. 1.   Drawing and photographs of larval stages of *Heterixalus rutenbergi* from Ambatomenaloha, Itremo, central Madagascar (a), drawing of a tadpole in life, based on a color photograph; (b), photograph of another tadpole specimen in life, (c), photograph of a metamorphosing juvenile (tail not yet fully reduced), already showing the typical adult coloration. Both photographs were made on 12 March 2001.

DISCUSSION

Assigning tadpoles to adult frogs is a difficult endeavour, and the decisions often remain tentative, except for cases in which (1) tadpoles are identified by means of genetic markers, (2) tadpoles are raised from clutches deposited by well-identified adult specimens, (3) metamorphosed juveniles are raised to the adult stage, (4) metamorphosed juveniles already show characters that are fully diagnostic for the particular species. The case of the tadpoles described herein belongs into the fourth category, and their assignment to *Heterixalus rutenbergi* is based on the following rationale (1) They have the typical *Heterixalus* tooth formula (see below) which is not found in any other group of Malagasy frogs (GLAW & VENCES 1994). (2) No other *Heterixalus* species is known from Itremo (GLAW & VENCES 1994), and during our survey we did not hear any call assignable to a *Heterixalus* species. (3) The larval color pattern on the flanks is different from that of the other known *Heterixalus* tadpoles, among which the only other species known to occur in the central highlands and adjacent western savannahs, *H. betsileo* and *H. luteostriatus*. (4) One specimen of the batch ZSM 789 2001 in stages 41-42 (forelimbs fully emerged, but larval mouthparts still present) still has the characteristic larval color pattern on the flanks but also shows a central, two
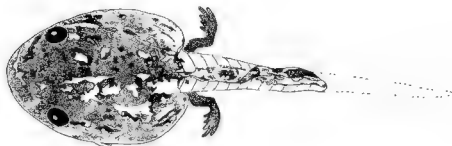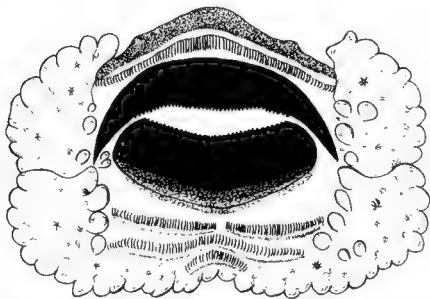
Fig. 2   Drawings of preserved tadpole specimen of *Heterixalus rutenbergi* from Ambatomenaloha, Itremo, central Madagascar, specimen LR 271 (developmenta. stage 37): (a) lateral view, (b) dorsal view, (c) mouthparts. Not to scale. Sharply delimited white patches in lateral and dorsal views symbolize detached skin.

dorsolateral and two lateral light stripes. (5) This five-striped pattern, which is fully developed in specimens in stages 45-46, is absent in all other *Heterixalus* and indeed also in all other Malagasy frog species (GLAW & VENCES, 1994), including all taxa reported from Itremo. Hence, this character reliably characterizes the tadpole specimens as *Heterixalus rutenbergi*

According to the data provided herein, general larval morphology of *H. rutenbergi* is similar to that of other *Heterixalus*. However, tadpoles of this species have a conspicuous color and distinct differences regarding the transition to the adult pattern. The adult coloration in *Heterixalus* is very diverse, and important differences can be observed within and among conspecific populations (GLAW & VENCES, 1993, 1994). Some species are characterized by a pair of light dorsolateral stripes. This pattern seems to be always present in adult *H. betsileo*, *H. carbonei* and *H. luteostriatus* (with the exception of *H. betsileo* from Ankaratra, in which the stripes are almost unrecognisable). Other species do not display this pattern as adults. However, two species of uniform adult coloration (*H. boettgeri* and *H. madagascariensis*) have dorsolateral stripes as juveniles, as do *H. andrakata*, *H. betsileo* and *H. "variabilis"* (GLAW & VENCES, 1993). *H. rutenbergi* differs from this trend because its five stripes appear simultaneously already at metamorphosis. Also the final color (dark green) was present from stage 45 onwards. This means that, in contrast to other *Heterixalus* species, a typical juvenile coloration is lacking in *H. rutenbergi*.

A second aspect that merits attention is the conspicuous silvery white marbling on the proximal portion of the tail of *H. rutenbergi* tadpoles. This pattern is not known from any other *Heterixalus* tadpoles (BLOMMERS-SCHLÖSSER, 1982; GLAW & VENCES, 1994), but it reminds the tadpoles of the African hyperolid genus *Kassina* that are also pond-dwellers (with very high fins, however) and display brightly striped or mottled patterns (e.g., CHANNING, 2001).

Heterixalus rutenbergi is known from six precise localities, all on the central high plateau of Madagascar: Ambohitantely, Mantasoa, Ambatolampy, Tsinjoarivo, Itremo and Ambatofitohararana (BLOMMERS-SCHLOSSER & BLANC, 1991; GLAW & VENCES, 1994; VALLAN, 2000) Because it is not a forest species, *H. rutenbergi* has not been recorded in most herpetological highland surveys, which did not focus on unforested areas. It seems clear, however, that the habitat choice of this species is more specialized than in its congeners that populate in huge densities all types of secondary habitats and even occur in flooded areas within towns. At Ambatolampy, we found *H. rutenbergi* in low densities in a moorland area, whereas *H. betsileo* was very common in the rice fields around the town (VENCES et al., 2002) At Mantasoa we were not able to confirm the presence of the species despite its characteristic calls that can be recognized over long distances (pers. obs.). Our findings in Itremo also refer to a relatively special highland savannah habitat. Certainly, the species is widespread over central Malagasy highlands, but its populations may have low densities and be vulnerable to transformation of moorland into rice fields. Additional fieldwork is needed to ascertain its habitat requirements and conservation status.

Acknowledgements

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Morfología del tubo digestivo en larvas de *Dermatonotus muelleri* y *Elachistocleis bicolor* (Anura, Microhylidae) del Noroeste argentino

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Morphology of the digestive tube in larvae of two species of Microhylidae from the Argentine Northwest, *Dermatonotus muelleri* and *Elachistocleis bicolor*, is described. The digestive tube length is standard, with two coiled nucleii in the midgut. Histologically the foregut presents a dorsal fold in the esophagus with many ciliated cells in the mucosae. The gastric region is characterized by a "manicotto glandulare" with a thick glandular layer. The epithelium of the midgut and posterior intestine is simple, showing columnar cells with brush border in the former and cylindric cells and caliciform cells in the latter. The anatomical characteristics of the coiling of the midgut have not been described for other larvae of neotropical Microhylidae, but the dorsal fold in the esophagus is common to other American microhylid genera.

Introducción

Las larvas de Microhylidae de vida libre se caracterizan por tener labios flexibles; el inferior puede ser protusible a modo de cuchara o en forma de embudo, en otros casos. La microfagia es el hábito alimenticio más común y las estructuras bucofaringeas colaboran en la captura de las partículas alimenticias. Orton (1953) clasifica a las larvas de Microhylidae como larvas de tipo II, las cuales presentan, entre otros caracteres, ausencia de piezas bucales queratinizadas, una cámara opercular simple y un espiráculo medio ventral. Altig & Johnston (1989) clasifican a algunas larvas de Microhylidae como suspensivoras de tipo I, con pliegues labiales semiesféricos sobre la boca, cuerpo muy deprimido y circular en vista dorsal.

Entre las descripciones de las estructuras orales internas en larvas de Microhylidae están las realizadas por Savage (1952) quien describió la anatomía de las estructuras bucofaringeas en larvas de cuatro especies de Microhylidae asiáticos (*Calluella guttulata, Glyphoglossus molossus, Chaperina fusca* y *Kaloula pulchra*). Wassersug (1980) en tres especies del género

Microhyla (*M. berdmorei*, *M. heymonsi* y *M. ornata*), WASSERSUG & PYBURN (1987) en *Otophryne robusta* que es un Microhylidae neotropical, entre otros autores. GRADWELL (1974) observó las estructuras branquiales en *Phrynomantis annectens*

La información referida al tubo digestivo en los Microhylidae neotropicales es inexistente. NELSON & CUELLAR (1968) realizaron estudios comparativos de la cavidad oral y del tubo digestivo en 4 especies de dos géneros de anuros americanos neárticos, *Hypopachus barberi*, *H. variolosus*, *Gastrophryne olivacea* y *G. usta*.

Existen dos especies de Microhylidae en el Noroeste argentino que son *Dermatonotus muelleri* y *Elachistocleis bicolor*. La morfología externa de la larva de *D. muelleri* fue descripta por CEI (1980) y ALTIG & JONHSTON (1986). LAVILLA (1992) re-describió la morfología externa de la larva y analizó el condrocráneo y el esqueleto visceral. De acuerdo con estas descripciones la larva presenta un cuerpo en vista dorsal cuadrangular y en vista lateral triangular, ojos pequeños dirigidos dorsolateralmente, una boca ventral, sin papilas marginales ni pico córneo, un espiráculo medial posterior cercano al tubo proctodeal, una cola triangular, gruesa y corta, con aletas dorsal y ventral delgadas.

Elachistocleis bicolor fue citada para otras zonas neotropicales por CEI (1980) y GUDYNAS (1983). WILLIAMS & GUDYNAS (1987) describieron la larva: presenta un cuerpo globoso, ojos pequeños que se ven dorsalmente, una boca pequeña, de ubicación anteroventral, con pliegues a modo de faldas y sin estructuras queratinizadas ni papilas marginales, un espiráculo terminal, inmediatamente por delante y a la izquierda de la abertura anal, una cola musculosa con aletas bajas que alcanzan el cuerpo.

Las estructuras orales internas en larvas de ambas especies fueron caracterizadas por ECHEVERRÍA & LAVILLA (2000).

LAVILLA & LANGONE (1991, 1995) describieron cambios ontogenéticos en la orientación del espiráculo y tubo proctodeal, así como las estructuras del condrocráneo en las larvas de *E. bicolor.*

En base a los antecedentes sobre el grupo de Microhylidae y la necesidad de contar con descripciones que posibiliten comparaciones intra e interfamiliares, se ha planteado el objetivo de este trabajo en la descripción del aparato digestivo post-faríngeo en las larvas suspensívoras micrófagas de Microhylidae que se encuentran en el Noroeste argentino.

MATERIAL Y MÉTODOS

Se utilizaron larvas de *Dermatonotus muelleri* y *Elachistocleis bicolor* entre los estadíos equivalentes a los 30-37 de la tabla de desarrollo normal de GOSNER (1960), provenientes de colectas realizadas en la localidad de Las Lajitas, Departamento Anta, Salta, Argentina, en el mes de enero de 1998 y de la colección del Museo de Ciencias Naturales de Salta MCN 123, respectivamente

El material se fijó en una solución de formaldehído al 10 % y se postfijo en líquido de BOUIN Las observaciones macroscópicas se hicieron por medio de disecciones bajo lupa, efectuando un corte en la línea media ventral para exponer el tubo digestivo

Tab. 1. – Morfometría del tubo digestivo en larvas de Microhylidae suspensívoras micrófagas (*Dermatonotus muelleri* y *Elachistocleis bicolor*). % sobre la longitud total del tubo digestivo.

Tubo digestivo	*Dermatonotus muelleri* (n = 7)	*Elachistocleis bicolor* (n = 7)
Longitud del tubo digestivo	8 ± 0.21 cm $\cong 10$ veces la longitud del cuerpo del renacuajo	4.45 ± 0.15 cm $\cong 6$ veces la longitud del cuerpo del renacuajo
Esófago	0.3 ± 0.01 cm = 3.750 %	0.1 ± 0.01 cm = 2.25 %
Manicotto glandulare	0.25 ± 0.01 cm = 3.12 %	0.15 ± 0.01 cm = 3.37 %
Intestino medio	5.95 ± 0.15 cm = 74.37 %	3.5 ± 0.11 cm = 78.65 %
Intestino posterior	1.5 ± 0.04 cm = 18.75 %	0.7 ± 0.02 cm ≈ 15.73 %

Los estudios morfométricos se realizaron en larvas equivalentes al estadio 35 de GOSNER (1960), se tomaron la longitud del cuerpo de cada renacuajo correspondiente a la medida entre el hocico y el vientre para comparar con el largo total del tubo digestivo y se midieron con un calibre Vernier cada porción del tubo digestivo. Las mediciones del intestino medio se realizaron sobre un papel milimetrado.

Para los estudios histológicos se extrajeron las distintas regiones del tubo digestivo, el material se deshidrató y se utilizó xilol como intermediario para su inclusión en paraplast. Se efectuaron cortes seriados de 6 µm de espesor con micrótomo de deslizamiento. La técnica de coloración utilizada fue Hematoxilina-Eosina (H&E). Las observaciones se efectuaron en microscopio estereoscópico Leica MPS30 y documentadas en cámara fotográfica fotoauto-mat MPS30.

RESULTADOS

DERMATONOTUS MUELLERI

Descripción anatómica

La longitud del tubo digestivo es aproximadamente diez veces la longitud del cuerpo (hocico-vientre) (tab. 1).

En *D. muelleri* el *esófago* se ubica en la línea media del cuerpo en la parte anterior de la cavidad abdominal, es relativamente corto y comprende un 3.75 % de la longitud total del tubo digestivo.

El *manicotto* glandulare está ubicado en la región dorsal de la cavidad, con paredes más gruesas y blanquecinas, y representa un 3.12 % de la longitud total del tubo digestivo (fig. 1A, C).
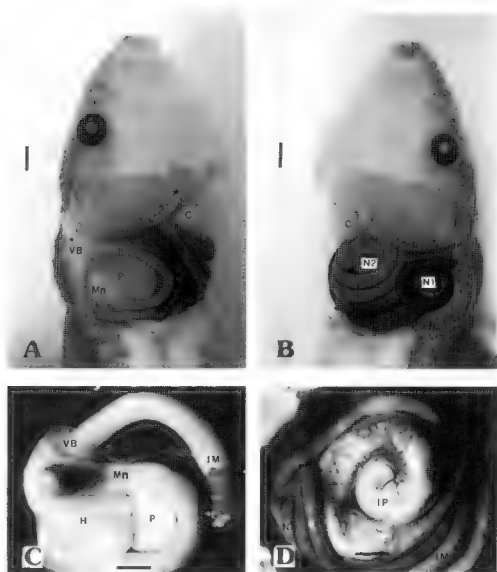
Fig. 1. - Tubo digestivo en *Dermatonotus muelleri*. (A) Vista lateral derecha de la cavidad abdominal. (B) Vista lateral izquierda de la cavidad abdominal. (C) Vista dorsal del intestino anterior. (D) Vista dorsal del intestino posterior. C, corazon; C H, conducto hepatico; F esofago; H, higado; I M, intestino medio; I P, intestino posterior; N, nucleo de enrollamiento; Mn, manicotto glandulare; P, pancreas; V B, vesicula biliar. Escala: 1 mm

La primera porción del intestino medio (duodeno) se curva alrededor del páncreas en el lado derecho El páncreas es mediano, de forma circular y color blanquecino, y el hígado está ubicación algo anterior al páncreas. El *intestino* medio es largo (74.37 º o de la longitud total del tubo digestivo) y ocupa gran parte de la cavidad abdominal Se caracteriza por presentar dos núcleos de enrollamiento. El primero es mas corto, teniendo 1.5 vueltas y está ubicado lateralmente en el lado izquierdo. El segundo es más largo, con 4.5 vueltas, ocupa la parte central de la cavidad y su eje está orientado en sentido dorso-ventral, ambos forman una espiral doble al enrollarse (fig. 1A-B).

El *intestino* posterior es más corto, presenta mayor diámetro y se enrolla internamente con posición más dorsal que el intestino medio. Representa un 18 75 % de la longitud total del tubo digestivo (fig. 1D).

Observaciones histológicas

Esófago

Presenta un septo longitudinal en la pared dorsal que abarca el primer tramo del esófago, tiene una submucosa con abundante tejido conectivo laxo y un epitelio con células cilíndricas ciliadas A ambos lados del septo, en la base del mismo, se encuentran células cilíndricas bajas secretoras de mucus.

El resto de la mucosa del esófago presenta una capa simple de células cilíndricas ciliadas y escasas células caliciformes en la pared ventral. La submucosa es una capa delgada de tejido conectivo laxo y la capa muscular es muy delgada con fibras circulares (fig. 2A-B).

En la porción posterior se forman varios plegamientos longitudinales con concentraciones de células cilíndricas secretoras de mucus en forma de penachos. La capa muscular es más gruesa con fibras circulares y externamente fibras longitudinales junto a la capa serosa (fig. 2C).

"Manicotto"

La mucosa tiene células cilíndricas secretoras de mucus con núcleo grande medio basal basófilo y citoplasma apical eosinófilo homogéneo Se alterna con escasas zonas de células cilíndricas ciliadas. La mucosa tiene un espesor de 15 µm.

El epitelio con células cilíndricas bajas de núcleo redondo basófilo puede estar interrumpido por la formación de criptas en algunas zonas. Las glándulas se disponen longitudinalmente con células cúbicas de núcleo redondo basófilo y citoplasma homogéneo eosinófilo. Esta capa tiene un espesor de 55 µm. Rodeando esta estructura se encuentran fibras musculares circulares y la serosa con un espesor de 2 5 µm (fig. 2D-E).

Intestino medio

Tiene un epitelio monoestratificado con abundantes células cilíndricas de borde estriado con núcleo redondo medial basófilo y citoplasma homogéneo eosinófilo y escasas células caliciformes, pequeñas y apicales La capa mucosa tiene un espesor de 15 µm y la muscular de 2.5 µm (fig. 2F).
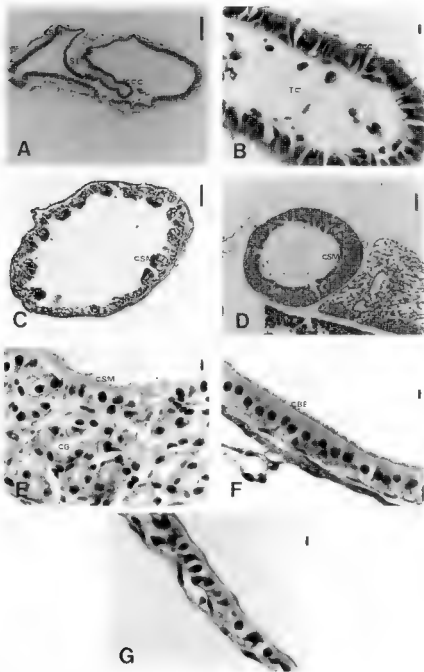
Fig. 2   Microfotografías del tubo digestivo en *Dermatonotus muelleri* (A) Esófago con septo longitudinal. Escala: 100 μm (B) Septo longitudinal. Escala: 5 μm (C) Esófago, zona de transición. Escala: 100 μm (D) Manicotto glandulare. Escala: 100 μm (E) Manicotto glandulare. Escala: 5 μm (F) Intestino medio. Escala: 5 μm (G) Intestino posterior. Escala: 5 μm. CCa, células caliciformes; CG, capa glandular; Cr, cripta; CBE, células cilíndricas cilidas, CSM, células secretoras de mucus; S.L, septo longitudinal; TC, tejido conectivo.

Intestino posterior

El epitelio es simple con células cilíndricas de núcleo redondo basófilo y citoplasma poco teñido, de 11 μm de espesor. La submucosa y la capa muscular son muy delgadas, y en total tienen 4 μm de espesor (fig. 2G).

ELACHISTOCLEIS BICOLOR

Descripción anatómica

El tubo digestivo presenta características semejantes a las descriptas en *D. muelleri*. La longitud total es algo mayor de seis veces la longitud del cuerpo. El esófago y el manicotto glandulare son porciones cortas del tubo digestivo y representan un 2.25 % y 3.37 % de la longitud total del tubo digestivo, respectivamente. La porción más larga es el intestino medio con un 78.65 % del largo total, al intestino posterior le corresponde un 15.73 % (tab. 1).

Observaciones histológicas

Esófago

Presenta un septo longitudinal en la pared dorsal con un epitelio monoestratificado de células cilíndricas ciliadas y células cilíndricas bajas secretoras de mucus en la base a ambos lados. En la pared ventral las células cilíndricas ciliadas se intercalan con células caliciformes. La submucosa forma una capa delgada de tejido conectivo laxo rodeada por una capa muscular muy delgada con fibras circulares (fig. 3A).

La zona posterior tiene pliegues con grupos de células cilíndricas secretoras de mucus en forma de penachos. La capa muscular a este nivel es más gruesa con fibras circulares y externamente fibras longitudinales junto a la capa serosa.

"Manicotto"

La mucosa tiene un epitelio simple con células cilíndricas bajas y escasas células ciliadas, ambos tipos de células están poco diferenciadas, con un espesor de 10 μm. Las glándulas se disponen longitudinalmente con células cúbicas de núcleo redondo basófilo y citoplasma homogéneo con poca afinidad a la eosina, formando una capa gruesa de 113 μm. Las fibras musculares circulares tienen un espesor de 2.5 μm (fig. 3B-C).

Intestino medio

Tiene un epitelio monoestratificado de 16 μm de alto, con abundantes células cilíndricas de borde estriado con núcleo redondo medial basófilo y citoplasma granular levemente eosinófilo y escasas células caliciformes. La capa muscular es más gruesa que en otras porciones del tubo digestivo y mide aproximadamente 8 μm de espesor (fig. 3D).
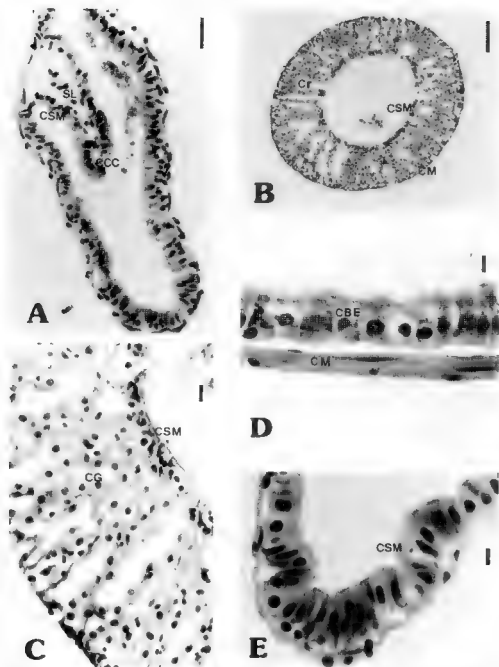
Fig 3 Microfotografías del tubo digestivo en *Elachistocleys bicolor* (A) Esófago con septo longitudinal Escala 25 μm (B) Manicotto glandulare Escala 100 μm (C) Manicotto glandulare Escala 25 μm (D) Intestino medio Escala 5 μm (E) Intestino posterior Escala 5 μm C G, capa glandular; C M, capa muscular; Cr, cripta; C B E, células de borde estriado; C C C, células cilíndricas ciliadas; C S M, células secretoras de mucus; S L, septo longitudinal

Intestino posterior

El epitelio es simple con células cilíndricas con núcleo redondo basófilo y citoplasma con gránulos eosinófilos, de 17 μm de espesor Las capas muscular y serosa son muy delgadas, con 5 μm de espesor (fig. 3E).

DISCUSIÓN Y CONCLUSIONES

Las dos especies de Microhylidae del Noroeste argentino estudiadas presentan a nivel del tubo digestivo caracteres morfológicos muy semejantes entre sí, coincidiendo con lo observado previamente por ECHEVERRÍA & LAVILLA (2000) con respecto a las estructuras internas de la cavidad oral.

La longitud del tubo digestivo en las larvas de *Dermatonotus muelleri* es de aproximadamente 10 veces la longitud del cuerpo del renacuajo y en *Elachistocleis bicolor* es más corto, representando 6 veces la longitud del cuerpo.

ALTIG & JOHNSTON (1989) clasifican a las larvas de varias especies de Microhylidae como formas que se alimentan de materia en suspensión, hábito que corresponde también para las especies aquí estudiadas. La presencia de todas estas características tanto de la cavidad oral como del tubo digestivo, corroboran el hábito alimenticio suspensívoro en estas especies, siendo de tipo micrófago

La escasa información disponible en relación con la estructura del tubo digestivo en larvas de Microhylidae neotropicales permite solamente comparar las observaciones realizadas en los géneros *Hypopachus* y *Gastrophryne* (NELSON & CUÉLLAR, 1968) y específicamente en *Hypopachus aquae* (SAVAGE, 1955), los cuales presentan a nivel del esófago el septo dorsal y en la región gástrica el "manicotto glandulare" (LAMBERTINI, 1929) con características muy semejantes a las observadas en las larvas de *D. muelleri* y *E. bicolor*.

La longitud del esófago en relación con el resto del tubo digestivo es muy corta, hecho que está relacionado con las especies suspensívoras (BARRINGTON, 1946, GRIFFITHS, 1961) También presenta una zona de transición entre el esófago y el manicotto glandulare, característica que comparte con Ranidae y Rhacophoridae (VIERTEL & RICHTER, 1999).

El manicotto glandulare en las larvas de ambas especies presenta estructuras una poco más complejas, en comparación con otras especies suspensívoras que lo presentan, como *Rana ridibunda* (GRIFFITHS, 1961) y *Pleurodema borellii* (ULLOA & TIRÁN, 1998) entre otras Las diferencias particularmente radican en la disposición de las glándulas tubulares y la presencia de numerosas criptas que interrumpen la continuidad de la capa epitelial Estas características también son compartidas con otras especies de Microhylidae (GRIFFITHS, 1961)

El intestino medio es la porción del tubo digestivo más larga y la característica más sobresaliente es la presencia de dos núcleos de enrollamiento. El primero es más pequeño y lateral, el segundo es más grande y ventral Esta característica no ha sido observada o descripta en formas de Microhylidae americanas (SAVAGE, 1955, NELSON & CUÉLLAR, 1968), ni en larvas de otras especies de anuros neotropicales (ULLOA KREISEL, 2001, ULLOA & TIRÁN,

1998; GIMÉNEZ et al., 1991, RADA & BELLO, 1988; JORQUERA et al , 1982), ni en observaciones propias realizadas en larvas de distintas especies de anuros del Noroeste argentino

El intestino posterior es más grueso y corto que el intestino medio, formado por un epitelio simple de células cilíndricas, una capa muscular muy delgada y serosa.

RESUMEN

Se describe la morfología del tubo digestivo en las larvas de dos especies de Microhylidae del Noroeste argentino, *Dermatonotus muelleri* y *Elachistocleis bicolor* La longitud del tubo digestivo es estándar, con dos núcleos de enrollamiento en el intestino medio. Histológicamente el intestino anterior presenta un pliegue dorsal en el esófago, con numerosas células cilíndricas ciliadas en la mucosa. La región gastrica tiene un "manicotto glandulare" con una espesa capa glandular. El epitelio del intestino medio y posterior es simple con células cilíndricas estriadas en el primero y células cilíndricas y caliciformes en el último Las características anatomicas del enrollamiento del intestino medio no han sido descriptas para otras larvas de Microhylidae neotropicales, pero el pliegue dorsal en el esófago es común a otros generos de microhylidos americanos.

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The "pseudofirmisternal"
pectoral girdle of anurans

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**The pectoral girdles of the following species were studied histologically:
(1) Brachycephalidae: *Brachycephalus ephippium*; (2) Bufonidae: *Atelopus subornatus*, *Frostius pernambucensis*, *Osornophryne bufoniformis*;
(3) Leptodactylidae: *Geobatrachus walkeri*, *Insuetophrynus acarpicus*;
(4) Pipidae: *Hymenochirus boettgeri*; (5) Ranidae: *Rana sylvatica*; (6) Rhinodermatidae: *Rhinoderma darwinii*. Of the non-ranoid frogs, only *A. subornatus*, *F. permanbucensis*, *H. boettgeri* and *O. bufoniformis* have completely fused, non-overlapping, epicoracoids (i.e., pseudofirmisterny). The girdle morphologies of *G. walkeri* and *R. darwinii* are unique in anurans. The girdles of *B. ephippium* and *I. acarpicus* are arciferofirmisternal. Morphological differences between the pseudofirmisternal and firmisternal girdles suggest they are not homologous.**

IINTRODUCTION

Pseudofirmisterny is the term describing the pectoral girdles of frogs, other than Ranoidea (i.e., Dendrobatidae, Hyperoliidae, Microhylidae, Ranidae and Rhacophoridae sensu FORD & CANNATELLA, 1993, or Hyperoliidae, Microhylidae, Ranidae, Mantellidae and Rhacophoridae sensu VENCES & GLAW, 2001), having the epicoracoid cartilages completely fused (i.e., from anterior to posterior) and not overlapping one another

The following genera of non-ranoid frogs are considered to have pseudofirmisternal girdles: *Brachycephalus* (including *Psyllophryne*, KAPLAN, 2002), *Atelopus*, *Frostius*, *Osornophryne*, *Atopophrynus*, *Geobatrachus*, *Insuetophrynus*, *Hymenochirus*, *Pseudhymenochirus* and *Rhinoderma* (BARRIO, 1970; TRUEB, 1973; RUIZ-CARRANZA & HERNANDEZ-CAMACHO, 1976; LYNCH, 1978; ARDILLA-ROBAYO, 1979; LYNCH & RUIZ-CARRANZA. 1982; CANNATELLA, 1985; 1986; DUELLMAN & TRUEB, 1985; MYERS & FORD, 1986; CANNATELLA & TRUEB, 1988; GRAYBEAL, 1997, however, see McLACHLAN, 1997; GRIFFITHS, 1957, 1963; McDIARMID, 1969) The non-ranoid, pseudofirmisternal family Dendrobatidae (LYNCH, 1973; HAY et al., 1995; FELLER & HEDGES, 1998; VENCES & GLAW, 2000, 2001) was not examined The above distribution of pseudofirmisterny in anurans is questionable, because only the girdles of *Brachycephalus ephippium* and *Rhinoderma darwinii* have been examined histologically and

observations of the pectoral girdle in cleared-and-stained specimens frequently are misleading (KAPLAN, 1993).

Generally, it is accepted that the character "epicoracoids completely fused and not overlapping one another" evolved independently in both non-ranoid and ranoid anurans (NOBLE, 1926; GRIFFITHS, 1963; DUELLMAN & TRUEB, 1985; FORD & CANNATELLA, 1993). Moreover, it is thought that this character evolved several times in non-ranoid frogs – viz., in *Insuetophrynus*, *Rhinoderma* and *Brachycephalus* (GRIFFITHS, 1963; LYNCH, 1978, DUELLMAN & TRUEB, 1985; FORD & CANNATELLA, 1993), in the ancestors of *Frostius*, *Atelopus* and *Osornophryne* (CANNATELLA, 1986; GRAYBEAL, 1997), in *Hymenochirus* and *Pseudhymenochirus* (CANNATELLA & TRUEB, 1988), and in *Atopophrynus* and *Geobatrachus* (MYERS & FORD, 1986). However, it is still unclear if these hypotheses are parsimonious, because there is no available cladistic analysis of the taxa with this girdle morphology. The character pseudofirmisterny supported the following monophyletic groups: *Brachycephalus* and *Atelopus* (GRIFFITHS, 1963), *Brachycephalus* and *Psyllophryne* (FORD & CANNATELLA, 1993), *Atelopus*, *Frostius* and *Osornophryne* (CANNATELLA, 1986; GRAYBEAL, 1997), and *Geobatrachus* and *Atopophrynus* (MYERS & FORD, 1986).

Herein, I describe the ventromedial parts of the pectoral girdles of most frogs that have been described as pseudofirmisternal, along with one having a firmisternal girdle – i.e., the pectoral girdles of ranoid frogs having the epicoracoids completely fused (FORD & CANNATELLA, 1993). The descriptions are based on examination of serial sections which were prepared to determine, first, whether the examined frogs have the epicoracoids completely fused and not overlapping, and second, whether the hypothesis that pseudofirmisterny evolved several times from firmisterny is consistent with the morphology (i.e., anatomical differences between non-ranoid and ranoid frogs). The systematic implications of these observations will be discussed

MATERIALS AND METHODS

The midventral parts of the breast shoulder apparatus of sexually mature individuals of the following families and species of frogs were sectioned: (1) Brachycephalidae *Brachycephalus ephippium* (UMMZ 103568), (2) Bufonidae *Atelopus subornatus* (ICN 15820), *Frostius pernambucensis* (UMMZ 225143), *Osornophryne bufoniformis* (ICN 11505), (3) Leptodactylidae *Geobatrachus walkeri* (ICN 35186), *Insuetophrynus acarpicus* (UMMZ 225142); (4) Pipidae *Hymenochirus boettgeri* (UMMZ 229751), (5) Ranidae *Rana sylvatica* (UMMZ 229752); (6) Rhinodermatidae *Rhinoderma darwinii* (UMMZ 143361). The medial part of the breast-shoulder apparatus was excised by cutting through the procoracoid cartilages, clavicles and coracoid bones; the epicoracoids and the attached prezonal and postzonal elements were removed, decalcified (Cal-Ex II, Fisher Scientific), embedded in paraffin (WEISSNER, 1960), sectioned transversely from the anterior tip of the omosternum to the posterior tip of the sternum, and stained with hematoxylin and eosin

The names of the muscles of *Atelopus subornatus*, *Brachycephalus ephippium*, *Hymenochirus boettgeri*, *Rana sylvatica* and *Rhinoderma darwinii* follow those in TYSON's (1987) and

BEDDARD's (1895, 1908) studies. The muscles of *Osornophryne bufoniformis*, *Frostius pernambucensis*, *Insuetophrynus acarpicus* and *Geobatrachus walkeri* are designated by numbers, as myological studies of these taxa are not available. Histological terminology follows that of FAWCETT (1986). Drawings of the girdles of *Atelopus farci* (KAPLAN, 1994) and *Pseudhymenochirus curtipes* (DE VILLIERS, 1929) are used instead of those of *A. subornatus* and *H. boettgeri* because the latter are not available.

Herein, I consider the epicoracoid cartilages to be the ventromedial elements of the girdle extending from the level of the clavicles to the coracoids, including the parts lying medial to the procoracoid shafts (GRIFFITHS, 1963; but see TYSON, 1987 and DUELLMAN & TRUEB, 1985) and the coracoid bones (i.e., the ossified portion of the embryonic coracoid-epicoracoid cartilage TYSON, 1987, KAPLAN, 1993), and anterior to the procoracoid (fig. 1); note that the medial position of the epicoracoids with respect to the procoracoid is assumed because they are indistinguishably fused in sexually mature individuals. I consider the epicoracoid horns to be the part of the epicoracoid cartilages that lie posterior to the posteromedial part of the coracoids. "Medial ligament" refers to the band of dense connective tissue ventromedial to the epicoracoids. The term "completely fused" refers to the fusion of the epicoracoids from their anterior to posterior tips. The term "fused" describes epicoracoids whose medial ends, or part of them, are united synchondrotically or by connective tissue that changes gradually from cartilage, near the epicoracoids, to dense regular connective tissue, at the midline. "Indistinguishably fused" is used to describe absence of a suture between the epicoracoids, where "suture" is defined as a thin, transverse band of cartilage with low cell, high fiber, densities, different coloration, and/or refractive properties. The epicoracoids are considered "overlapping" when every part of their medial ends are aligned with one another on the vertical axis. The descriptors "left" and "right" refer to the organism's left and right sides from the dorsal perspective.

Developmental stages are given according to GOSNER (1960). The following abbreviations are used to designate the collections where the specimens studied are kept: ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogota, Colombia; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.

RESULTS

BRACHYCEPHALUS EPHIPPIUM

Anteriorly (fig. 2, 3A), the epicoracoids (e) are fused indistinguishably to one another on the midline at the level of the clavicle (cl). Slightly posterior (fig. 3B), there is a suture (su) between the epicoracoids. Posteriorly (fig. 3C), the epicoracoids are marked by a shallow dorsomedial crevice (cr) and a broad ventromedial keel (k), loose regular connective tissue fills the crevice. The *m. supracoracoideus* (msc) inserts on the ventral keel, medial ligament (ml) and ventral surfaces of the procoracoids (p). Posterior to the procoracoids (fig. 3D), two flat, expanded coracoids (co) flank the epicoracoids; the medial end of each coracoid has a cartilaginous core, that is indistinguishable from the epicoracoids, surrounded by a bony layer. Posteriorly (fig. 3E), the epicoracoids are free, the left side of the ventral keel is replaced
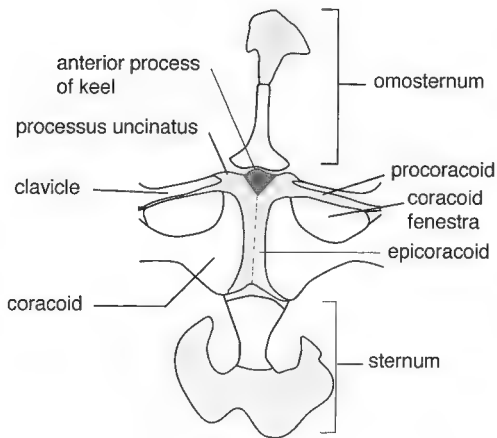
Fig. 1. – The ventral elements of the pectoral girdle of *Rana sylvatica* (adapted from Tyson, 1987). Dashed mid line: medial edge of epicoracoids; light gray: cartilage; dark gray: loose connective tissue; white: bone
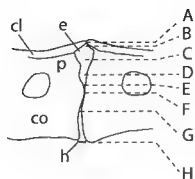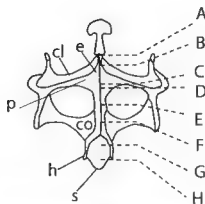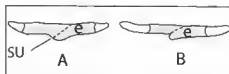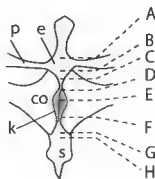
Brachycephalus ephippium
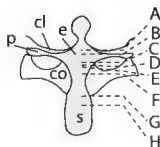
Rhinoderma darwinii

Insuetophrynus acarpicus

Geobatrachus walkeri

Fig. 2   Ventral view of the pectoral girdle of *Brachycephalus ephippium* (adapted from TYSON, 1987), *Rhinoderma darwinii* (adapted from CEI, 1980), *Insuetophrynus acarpicus* (adapted from BARRIO, 1970) and *Geobatrachus walkeri* (adapted from ARDILLA-ROBAYO, 1979). cl, clavicle; co, coracoid; e, epicoracoid; h, epicoracoid horn; p, procoracoid; s, sternum; su, suture. White: bone; light gray: cartilage; dark gray: area where the coracoids and epicoracoids are desorganized. A-H transverse sections corresponding to those of fig. 3-6. A and B in insert: transverse sections corresponding to those of fig. 4D-E
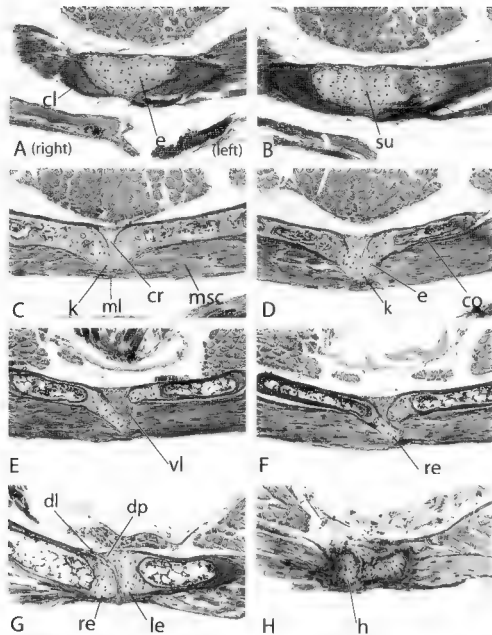
Fig. 3. – Histological cross sections, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of an adult *Brachycephalus ephippium* (UMMZ 103568). The levels of the sections are indicated in fig. 2. cl, clavicle; co, coracoid; cr, crevice; dl, dorsal ligament; e, epicoracoids; h, epicoracoid horn; k, ventral keel; le, left epicoracoid; msc, *m. supracoracoideus*; re, right epicoracoid; su, suture; vl, ventral ligament.

by dense, regular connective tissue termed the ventral ligament (vl). The *m. supracoracoideus* inserts on the ventral ligament. Posteriorly (fig. 3F), the right epicoracoid (re) slightly overlaps the left epicoracoid (le). The left epicoracoid abuts against the dorsomedial surface of the right epicoracoid. At the midlevel of the coracoids (fig. 3G), the left epicoracoid bears a small dorsal process (dp) that overlaps the right epicoracoid, a dorsal ligament (dl) joins this dorsal process to the dorsomedial surface of the right coracoid. Each epicoracoid terminates in a minute horn (h) (fig. 3H). The *m. sternoepicoracoideus* inserts on the posterior terminus of the horn.

RHINODERMA DARWINII

Anteriorly (fig. 2, 4A), the epicoracoids (e) are indistinguishably fused at the midline. The *m. supracoracoideus* (msc) inserts on the ventromedial surface of the clavicles, epicoracoids and medial ligament (ml). A small ventral keel (k) is present posteriorly (fig. 4B). The coracoids laterally flank the epicoracoids (fig. 4C). An oblique suture (su) separates the epicoracoids (fig. 4D). Posteriorly, a triangular notch (n) in the right side of the ventral keel is filled with loose connective tissue (fig. 4E); the *m. supracoracoideus* inserts on this connective tissue, the ventral surfaces of the right epicoracoid and the medial ligament. At the level of the coracoids (fig. 4F), the loose connective tissue in the notch is replaced by cartilage (x). Posteriorly (fig. 4G), each epicoracoid terminates in a horn (rh) that curves posterolaterally. The horns and the sternum (s) are separated by sutures. Posteriorly (fig. 4H), the *m. sternoepicoracoideus* (mse) inserts on the posterior ends of the epicoracoid horns.

INSUETOPHRYNUS ACARPICUS

The anterior epicoracoids are indistinguishably fused to one another at the midline (fig. 2, 5A), but slightly posteriorly (fig. 5B) the epicoracoids can be distinguished from one another, each bears a dorsomedial protuberance (dp). There is a distinct dorsomedial crevice and a rounded, ventromedial keel (k). *Muscle 1* (m1) inserts on the lateral surface of each epicoracoid and *Muscle 2* (m2) on the ventrolateral surface and medial ligament (ml). The dorsal crevice is extended ventrally as a sigmoid shape, the dorsal part of the left epicoracoid slightly overlaps the right epicoracoid (fig. 5C). *Muscle 3* (m3) inserts on the ventral part of the medial ligament. In the anterior region of the coracoid fenestra (fig. 5D), the epicoracoids are free; the medial end of the left epicoracoid (le) is wide, and overlaps the right epicoracoid (re). The left side of the ventral keel is replaced by dense, regular connective tissue, the ventral ligament (vl), on which *muscle 2* inserts. Posteriorly (fig. 5E), the left epicoracoid is triangular in section and the right epicoracoid elliptical. The right epicoracoid abuts against the ventral ligament and dorsal ligament (dl) extends between the medial end of the left epicoracoid and the right epicoracoid. *Muscle 2* inserts on the ventral ligament and the lateral surface of each epicoracoid. *Muscle 3* inserts mostly on the medial ligament. At the level of the coracoids (fig. 5F), a gap separates the medial ligament (ml) and the right epicoracoid (re), which overlaps the left extensively. The epicoracoids terminate in a pair of horns (fig. 5G), each of which lies in a lateral sternal groove (sg). Parts of the horns are fused to the sternum. A laterally directed ligament (ll) inserts on the posterior tips of the epicoracoid horns (fig. 5H); a *m. sternoepicoracoideus* is not evident.
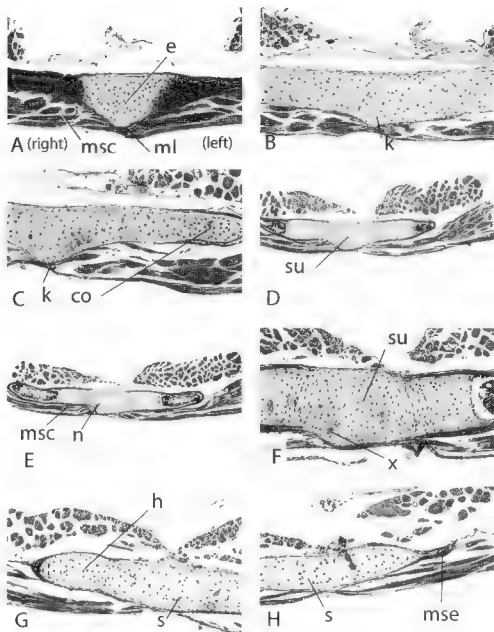
Fig. 4   Histological cross sections, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Rhinoderma darwini* (UMMZ 143361). The levels of the sections are indicated in fig. 2. co, coracoid; e, epicoracoids; h, epicoracoid horn; k, keel; ml, medial ligament; msc, *m. supracoracoideus*; mse, *m. sternepicoracoideus*; n, notch at the right side of the ventral keel; s, sternum; su, suture; x, part of the ventral keel replaced by cartilage
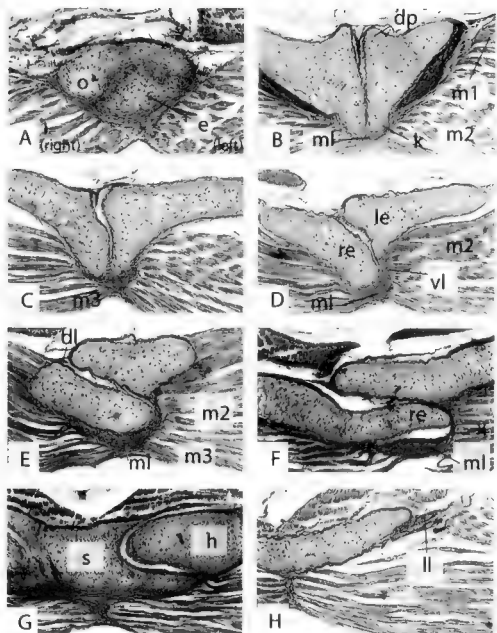
Fig 5 Histological cross section in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Insuctophrynis acarpicus* (L MMZ 228142) The levels of the sections are indicated in fig 2 dl dorsal ligament, dp dorsal protuberances, e epicoracoids, h epicoracoid horns, k, keel, le left epicoracoid ll, lateral ligament, m1, *muscle 1* m2 *muscle 2* m3 *muscle 3* ml medial ligament o, omosternum, re, right epicoracoid; s, sternum; vl, ventral ligament

GEOBATRACHUS WALKERI

Anteromedially (fig. 2, 6A), the epicoracoids (e) are indistinguishably fused to one another. *Muscle 1* (m1) inserts on the lateral and ventral surfaces of the epicoracoids and on the medial ligament (ml). Posterior to the procoracoids (fig. 6B), the fused epicoracoids bear a shallow dorsomedial depression. Slightly posteriorly (fig. 6C), the coracoids (co) lie lateral to the epicoracoids, which are separated by a suture (su) marked by a shallow dorsomedial depression. *Muscle 1* is divided into a wide slip, *muscle 1a* (m1a) that inserts on the coracoids, and a thin slip, *muscle 1b* (m1b) that inserts on the medial ligament. At the level of the coracoid shafts (fig. 6D), an ovoid ventral keel (k) is evident. The epicoracoids bear a shallow dorsomedial crevice; only *muscle 1b* is evident. Slightly posteriorly (fig. 6E), only the ventral keel remains. The medial parts of the coracoids are replaced by a membrane (me). *Muscle 1b* inserts on the lateral and dorsolateral surfaces of the keel and on the medial ligament. Posteriorly (fig 6F), the epicoracoids and medial part of the coracoids are evident and the ventral keel is small. Posteriorly (fig. 6G), the epicoracoids diverge slightly from one another, and *muscle 3* (m3) inserts on their dorsal surfaces. At the posterior terminus (fig 6H), the epicoracoids and sternum are indistinguishably fused; neither epicoracoid horns nor the *m. sternoepicoracoideus* is evident.

ATELOPUS SUBORNATUS

Anteromedially (fig. 7A-B), the epicoracoids (e) are indistinguishably fused to one another. Posteriorly (fig. 7C), a small, triangular ventral keel (k) is evident. At the anterior level of the coracoids (fig. 7D), the fused epicoracoids are oval in cross section and the *m supracoracoideus* (msc) inserts on the medial ligament (ml) and ventrolateral surfaces of the epicoracoids, the *m coracoradialis* (mcr) on their dorsolateral and dorsal surfaces. Posteriorly (fig 7E), the coracoids laterally flank the epicoracoids, which are represented by two ovoid elements that are fused medially. The *m. rectus abdominis* (mra) inserts on the dorsomedial surfaces of the epicoracoids. At the posterior level of the coracoids (fig 7F), the epicoracoid horns (h) diverge from one another. The horns are fused partially to the sternum (s) and sternal grooves are evident. The *m. sternoepicoracoideus* is absent.

OSORNOPHRYNE BUFONIFORMIS

Anteromedially (fig. 8, 9A-B), the epicoracoids (e) are indistinguishably fused to one another. Slightly posteriorly (fig 9C), a suture (su) separates the epicoracoids and a small, triangular ventral keel (k) is evident. *Muscle 1* (m1) inserts on the ventral surface of each clavicle (cl) and the medial ligament (ml). Posteriorly (fig. 9D), the epicoracoids bear a shallow, dorsomedial crevice and a rounded ventromedial keel. *Muscle 1* inserts on the ventromedial surfaces of the procoracoids, lateral surfaces of epicoracoids and medial ligament. At the level of the coracoid fenestra (fig 9E), the epicoracoids are expanded (i e, bladelike), flat, and slightly curved. *Muscle 1* inserts on the ventral surfaces of the epicoracoids and medial ligament. An oblique suture (su) separates the two epicoracoids such that the left epicoracoid bears the ventral keel. Between the coracoids (fig 9F), the epicoracoids
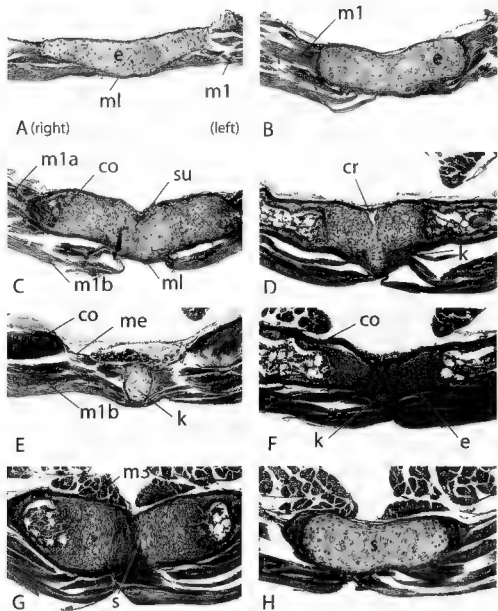
Fig 6 Histological cross section, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Geobatrachus walkeri* (ICN 35,86) The levels of the sections are indicated in fig 2 co, coracoid; cr, crevice; e, epicoracoids; k, keel; ml, *muscle 1*, m1a, *muscle 1a*; m1b, *muscle 1b*, me, membrane; ml, medial ligament; s, sternum; su, suture.
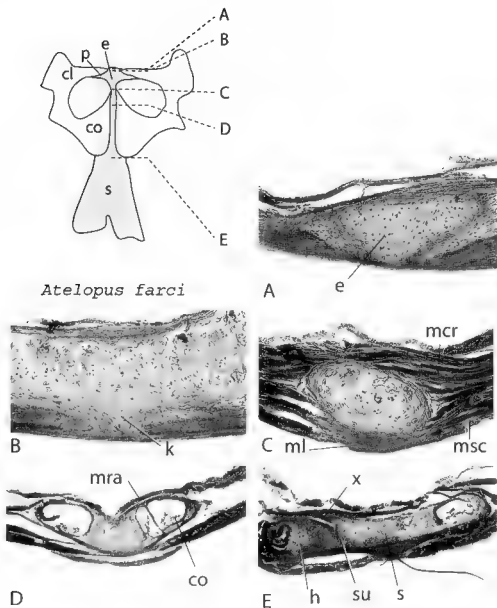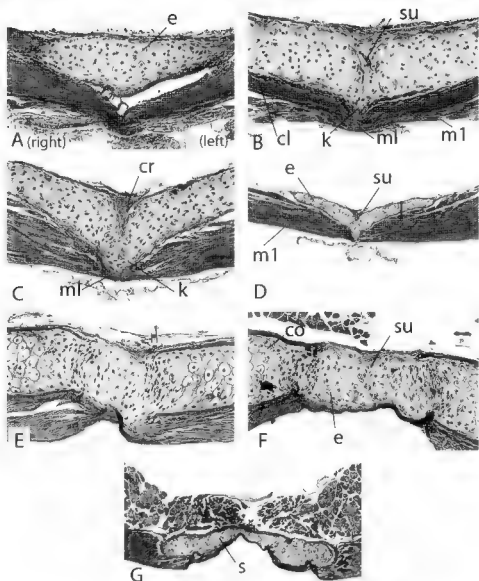
Atelopus farci

Fig. 7   Ventral view of the pectoral girdle of *Atelopus farci* (adapted from KAPLAN, 1994) and histological cross sections, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Atelopus subornatus* (ICN 15820). cl, clavicle; co, coracoid; e, epicoracoid; h, epicoracoid horns; k, keel; mra, *m. rectus abdominis*; mcr, *m. coracoradialis*; ml, medial ligament; msc, *m. supracoracoideus*; p, procoracoids; s, sternum; su, suture; x, gap. Gray cartilage, white bone. A-E corresponding transverse sections of drawing and photos.
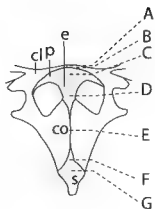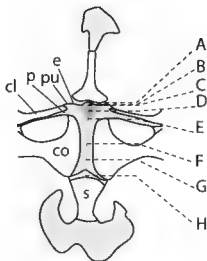
Osornophryne bufoniformis   *Rana sylvatica*
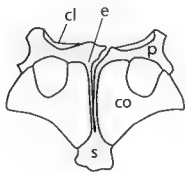
Atopophrynus syntomopus

Fig 8   Ventral view of the pectoral girdle of *Osornophryne bufoniformis* (adapted from Ruiz-Carranza & Hernández Camacho, 1976), *Rana sylvatica* (adapted from Tyson, 1987) and *Atopophrynus syntomopus* (adapted from Myers & Ford, 1986) cl, clavicle, co, coracoid, e, epicoracoid, p, procoracoid, pu, *processus uncinatus*, s, sternum. Light gray cartilage; dark gray loose connective tissue; white; bone. A-H: transverse sections corresponding to those of fig. 9-10

Fig. 9. — Histological cross sections, in an antero posterior direction, of the ventromedial part of the pectoral girdle of *Osornophryne bufoniformis* (ICN 11505). The levels of the sections are indicated in fig. 8. co, coracoid; cl, clavicle; e, epicoracoid; cr, crevice; k, keel; m1, *muscle 1*; ml, medial ligament; s, sternum; su, suture.

are indistinguishably fused and lack both, a ventral keel and dorsal crevice. Posteriorly (fig. 9G), a suture separates the epicoracoids. At the level of the sternum (fig 9H), the epicoracoids are indistinguishably fused to this structure. Neither epicoracoid horns nor the *m. sternoepicoracoideus* are present.

RANA SYLVATICA

Anteriorly (fig. 8, 10A), the ventral keel of the epicoracoids bears a process (kp) that lies in the biforated base of the omosternum (o). Slightly posteriorly (fig 10B), the anterior protuberance (pu) of each epicoracoid (i.e., *processus uncinatus*: FUSCH, 1926) laterally flanks the omosternum. In posterior sections (fig. 10C), the keel process is joined with the *processus uncinatus* Near the anterior levels of the coracoid fenestra (fig 10D), the epicoracoids bear a dorsomedial crevice (cr). The *m. supracoracoideus* (msc) inserts on the ventral keel and the *m coracoradialis* (mcr) on the ventral surfaces of the clavicles. Posterior to the procoracoids (fig. 10E), the coracoids (co) flank laterally the epicoracoids and the epicoracoids are fused ventrally The *m. coracoradialis* inserts on the lateral surface of each coracoid. At the midlevel of the coracoids (fig. 10F), the epicoracoids are surrounded by bone and, except medially and ventrally, they are eroded; the ventral keel (k) remains cartilaginous Posteriorly (fig. 10G), a suture (su) separates the ventral keel and the epicoracoids. Posteriorly (fig 10H), the ventral keel is replaced by the sternum (s) which is united synchondrotically with the keel. The posterior termini of the epicoracoids diverge as horns (h), which are surrounded by bone and fused to the dorsolateral parts of the sternum and to one another by a dorsal osseous bridge

HYMENOCHIRUS BOETTGERI

Anteromedially (fig 11A-B), the epicoracoids (e) are indistinguishably fused to one another. At the anterior level of the coracoid fenestra (fig. 11C), the epicoracoids are wide, flat and expanded in cross section. The *m coracoradialis* (mcr) inserts on the lateral and ventrolateral surfaces of the epicoracoids. At the midlevel of the coracoid fenestra (fig 11D), the epicoracoids are narrower Posterior to the coracoids (fig. 11E), the epicoracoids diverge laterally as two epicoracoid horns. These horns have densely packed chondrocytes and are fused to the sternum (s). The *m. sternoepicoracoideus* is absent.

FROSTIUS PERNAMBUCENSIS

Anteromedially (fig 12A), the epicoracoids (e) are indistinguishably fused to one another. *Muscle I* (ml) inserts on the ventromedial surface of each clavicle (cl) Posteriorly (fig. 12B), a suture separates the epicoracoids. Posterior to the procoracoids (fig 12C), the epicoracoids are small and ovoid in sections and bear a dorsomedial depression *Muscle I* inserts on the lateral, dorsolateral and ventrolateral surfaces of the epicoracoids and medial ligament (ml) At the level of the coracoid (fig. 12D), the *m rectus abdominis* (mra) inserts on the dorsomedial surface of the epicoracoids Posteriorly (fig 12E), the epicoracoids horns
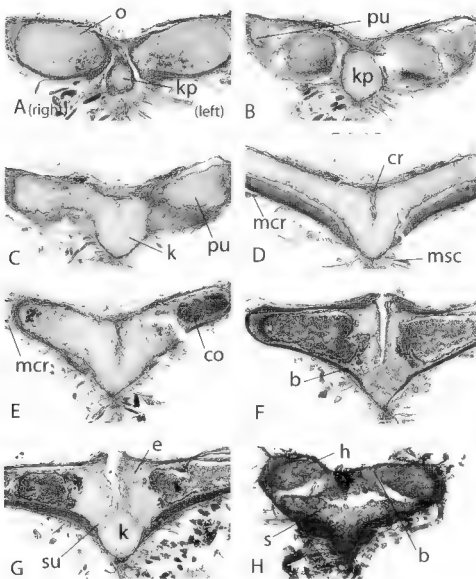
Fig 10   Histological cross section, in an antero posterior direction, of the ventromedial part of the
pectoral girdle of *Rana sylvatica* (UMMZ) The levels of the sections are indicated in fig 8 b, bone,
co, coracoid; cr, crevice, e, epicoracoid, h, epicoracoid horn, k, keel, kp, keel process, mcr, *m
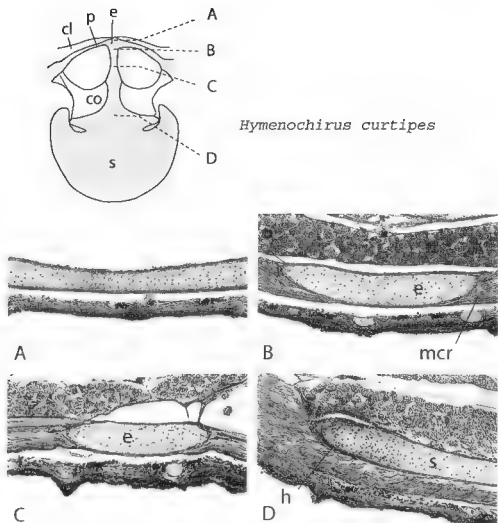coracoradialis*, msc, *m. supracoracoideus*; o, omosternum; pu, *processus uncinatus*, s, sternum, su,
suture

Hymenochirus curtipes

Fig 11 Ventral view of the pectoral girdle of *Hymenochirus curtipes* (adapted from De VILLIERS, 1929) and histological cross section, in an antero posterior direction, of the ventromedial part of the pectoral girdle of *Hymenochirus boettgeri* (UMMZ) cl, clavicle; co, coracoid; e, epicoracoid; h, epicoracoid horn; mcr *m coracoidalis*; p, procoracoid; s, sternum Gray cartilage, white bone A-D, corresponding cross sections of drawing and photos.
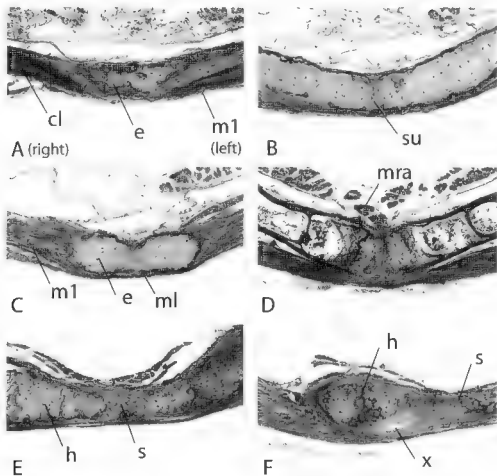
Fig. 12   Histological cross section, in an antero-posterior direction, of the ventromedial part of the
pectoral girdle of *Frostius pernambucensis* (UMMZ 225143). cl, clavicle, e, epicoracoid, h, epicora
coid horn, m1, *muscle 1*, mra, *m. rectus abdominis*, ml, medial ligament, s, sternum, su, suture, x, gap.

diverge from one another. The sternum and horns, which have different coloration and cell densities, are fused to one another Posteriorly (fig 12F), gaps separate the horns and sternum. The *m. sternoepicoracoideus* is absent.

DISCUSSION

Of the pectoral girdles studied, only those of *Atelopus subornatus*, *Frostius pernambucensis*, *Hymenochirus boettgeri*, *Osornophryne bufoniformis* and *Rana sylvatica* have completely fused, non-overlapping epicoracoids However, the epicoracoids of each of these taxa, except *O bufoniformis*, diverge slightly from one another posterior to the coracoids and, thus, are not fused throughout their entire lengths. The condition in *Atopophrynus* and *Pseudhymenochirus* is unknown The epicoracoids of *Geobatrachus walkeri* are completely fused and not overlapping except for a small area at the level of the coracoid shafts. At this level, the structure of the epicoracoids and medial part of the coracoids is disorganized; this morphology is unique in anurans.

In *Rhinoderma darwinii*, the epicoracoids are indistinguishably fused and not overlapping anterior to the midlevel of the coracoid fenestra, but fused (i.e., through their overlapping surfaces, rather than the medial ends) and overlapping posterior to this level. GRIFFITHS (1957, 1963) considered the overlap of the epicoracoids to start posterior to the coracoids, whereas KAPLAN (1993) thought that it started at the posterior level of the procoracoids. The overlap of the epicoracoids is evident in froglets (stage 46) (KAPLAN, 1993); however, in sexually mature individuals, it is evidenced only by the presence of an oblique medial suture and a free (i e., unfused) medial epicoracoid margin (fig. 2A-B) The girdle morphology in which the epicoracoids are fused and overlapping in the same cross section, and where the fused parts are their overlapping surfaces, rather than their medial ends, is unique in anurans.

In *Brachycephalus ephippium*, the epicoracoids are fused without overlap from their anterior tips to the posterior level of the coracoid fenestra, posterior to this level, they are free (i.e., attached by dense connective tissue) and overlapping The girdle of *B ephippium* is arciferofirmisternal viz, epicoracoids fused to, and not overlapping, one another from their anterior tips to a level posterior to the clavicles and free, and overlapping, posteriorly to this point (DUELLMAN & TRUEB, 1985). However, the girdle of *B ephippium* differs from other arciferofirmisternal girdles (e g., *Dendrophryniscus*, *Melanophryniscus*) in having a very reduced area where the epicoracoids are fused and overlapping.

TRUEB (1973) and FORD & CANNATELLA (1993) argued that *Brachycephalus* has completely ossified epicoracoids, this study shows that the epicoracoids are cartilaginous (i e , by definition, the epicoracoids are the cartilagınous remnant of the embryonic coracoidepicoracoid cartilage. FUSCH, 1926, TYSON, 1987; KAPLAN, 1993) TRUEB (1973) considered the epicoracoids to be juxtaposed, rather than fused, in *B ephippium* My results indicate that the epicoracoids are fused to one another up to the anterior level of the coracoids, and firmly attached to one another posterior to this level.

The girdle of *Insuetophrynus acarpicus* is arciferofirmisternal, because the non-overlapping epicoracoids are fused from their anterior tips to the posterior level of the procoracoids They are unfused and overlapping posterior to this level.

The girdles of *Atelopus subornatus*, *Frostius pernambucensis*, *Hymenochirus boettgeri* and *Osornophryne bufoniformis* differ from those of *Rana sylvatica* and *Hoplobatrachus chinensis* (often referred to as *Rana rugulosa*, but see KOSUCH et al., 2001) (KAPLAN, 2000) by having the most anterior parts of the epicoracoids in contact with one another and indistinguishably fused. In *R. sylvatica* and *H. chinensis*, the anterior epicoracoids (i.e., the *processus uncinatus*, because the anterior process of the ventral keel is of sternal origin; KAPLAN, 1993) are free (i.e., attached by dense connective tissue) and diverging from one another. This observation is consistent with the hypothesis that pseudofirmisterny and firmisterny evolved independently, however, it is still unknown whether the girdle morphologies of *R. sylvatica* and *H. chinensis* are widespread among Ranoidea. The characteristic girdle morphology known long ago in *Hoplobatrachus* and related groups (BOLKAY, 1915) and referred to as "arcizony" (DECKERT, 1938) or "arciferal-like condition" (TRUEB, 1973: 95) is a variant of firmisterny and has nothing to do with pseudofirmisterny.

The girdles of *Atelopus subornatus* and *Hymenochirus boettgeri* differ from those of *Frostius pernambucensis* and *Osornophryne bufoniformis* by having the epicoracoids indistinguishably fused. DE VILLIERS (1929) incorrectly stated that in *Hymenochirus* the epicoracoids are separated by a suture. In *F. pernambucensis* and *O. bufoniformis*, the epicoracoids are indistinguishably fused to one another from their anterior tips to the posterior level of the procoracoids and separated by a suture posterior to this level. These differences are minimal, and it is still unknown whether the presence or absence of suture between the epicoracoids is the result of ontogenetic and/or intraspecific variation. Therefore, the structural homology of the girdles of *A. subornatus*, *F. pernambucensis*, *H. boettgeri* and *O. bufoniformis* is equivocal.

I found several morphological differences among the girdles of the non-ranoid frogs studied. The epicoracoids are expanded and flat in *Hymenochirus boettgeri* and *Osornophryne bufoniformis*, but not expanded and ovoid in *Frostius pernambucensis* and *Atelopus subornatus*. No muscle inserts on the dorsal and lateral surfaces of the epicoracoids in *O. bufoniformis*, but they do on the lateral and dorsal surfaces in *A. subornatus* and *F. pernambucensis* and in the lateral surfaces in *H. boettgeri*. In *O. bufoniformis*, a suture separates the epicoracoids asymmetrically whereas this separation is symmetrical in *F. pernambucensis*. The systematic value of these characters is unknown.

The hypothesis that pseudofirmisterny is a synapomorphy uniting *Brachycephalus* and *Atelopus* (GRIFFITHS, 1963) and *Brachycephalus* and *Psyllophryne* (FORD & CANNATELLA, 1993) is false because *B. ephippium* lacks this character. Similarly, pseudofirmisterny does not support the monophyly of *Geobatrachus* and *Atopophrynus* because *Geobatrachus* lacks this character. Moreover, the girdles of these two taxa differ externally, as is evident by comparison of figures 2 and 8.

The character "epicoracoids completely fused to, and not overlapping, one another" unites only *Atelopus*, *Frostius* and *Osornophryne*. However, there are morphological differences among their girdles (e.g., epicoracoids indistinguishably fused or partially separated by a suture, symmetrically or asymmetrically separated by a suture, expanded or not expanded) that may be phylogenetically informative.

RESUMEN

Se estudiaron histologicamente las cinturas pectorales de las siguientes especies: *Atelopus subornatus*, *Brachycephalus ephippum*, *Frostius pernambucensis*, *Geobatrachus walkeri*, *Hymenochirus boettgeri*, *Insuetophrynus acarpicus*, *Osornophryne bufoniformis*, *Rana sylvatica*, *Rhinoderma darwini*. Dentro de los anuros no ranoideos estudiados, solamente *A. subornatus*, *F. permambucensis*, *H. boettgeri* y *O. bufoniformis* presentan los cartílagos epicoracoidales completamente fusionados y sin sobrelaparse (i e., pseudofirmisternia). Las cinturas pectorales de *G. walkeri* y *R. darwini* son únicas dentro de los anuros. Las cinturas pectorales de *B. ephippum* y *I. acarpicus* son arciferofirmisternales. Las diferencias morfológicas entre las cinturas pectorales firmisternales y pseudofirmisternales sugieren que estas no son homólogas.

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Comments on a new book on the Amphibia of Thailand, with a tentative allocation of the figured species

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Amphibians of Thailand by Wirot Nutphund is a nice book, with numerous colour drawings and photos for many of the Thai species. For each of them the author gives scientific, English and Thai name, followed by a short description, notes on ecology and distribution data. He also presents drawings of eggs and tadpoles of various species. However, beside its very nice aesthetic aspect, this book contains many errors. As it is sold in general book stores and on internet, and will be purchased by many people, I decided to publish corrected legends to photos. For many photographs it is not possible to allocate species, so only generic names are given. These tentative allocations, presented in table 1, are exclusively done for the species figured on a photo (NUTPHUND, 2001: 60-177). Drawings of this book, that show a more artistic than scientific expression, have not been studied. The valid names of all species with their author and date of publication are given for allocated species (for ranids, see DUBOIS, 1992).

ADDITIONAL COMMENTS

The photo p. 103 (NUTPHUND, 2001) shows a particular colour morph of *Rana erythraea* with a fine, indistinct mid-dorsal line (BOURRET, 1942: 331). The overall colour of the frog is darker than the usual bright grass green.

The photo p. 149 (NUTPHUND, 2001) represents an interesting colour mutation, resulting in a beautiful sky blue frog with orange webbing on hand and feet and small white dots on the back. This blue colour was found in other species of frogs like in *Rana synkl. esculenta* Linnaeus, 1758 and *Hyla arborea* (Linnaeus, 1758). It is due to absence of yellow xanthophores in the skin. The frog can with no doubt be allocated to *Rhacophorus bipunctatus* Ahl, 1927.

BOURRET (1942) described a subspecies *Kaloula pulchra macrocephala* (syntypes, Hanoi University B.35, adult male, B.36 adult female: type-locality Indochina) showing moistinct dorsolateral bands and mid-dorsum covered by large-sized irregular patches. The holotype by monotypy of *Kaloula aureata* Nutphand, 1989 (MNHN 1997.1923, adult male SVL 59.9 mm after preservation, donated by Nutphund to the Paris Museum, type-locality Thang Song District, Nakhon S. Thammarat, Thailand) is figured p. 163 (NUTPHUND, 2001) and shows a similar dorsal pattern as the holotype of *Kaloula pulchra macrocephala*. The name *Kaloula aureata* Nutphand, 1989 is here tentatively considered a subjective junior synonym of *Kaloula macrocephala* Bourret, 1942.

Table 1   Tentative allocation of specific names to photographs of Amphibia in NUTHPUND (2001)

Page	Name in NUTHPUND (2001)	Corrected name
60	*Tylototriton verrucosus*	*Tylototriton verrucossus* Anderson, 1871
61	*Ichthyophis kohtaoensis*	*Ichthyophis kohtaoensis* Taylor, 1959
64-65	*Bufo melanostictus*	*Bufo melanostictus* Schneider, 1799
71	*Bufo asper*	*Bufo asper* (Gravenhorst, 1829)
72	*Bufo macrotis*	*Bufo macrotis* Boulenger, 1887
73	*Bufo parvus* [sic]	*Bufo parvus* Boulenger, 1887
74	*Ansonia malayana*	**Bufo asper** (Gravenhorst, 1829), juvenile
75	*Pedostibes hosii*	*Pedostibes hosii* (Boulenger, 1892)
76	*Leptobrachium hasseltii*	**Micrixalus inornata** (Boulenger, 1890)
77	*Leptobrachium hendricksoni*	*Leptobrachium hendricksoni* Taylor, 1962
79	*Leptobrachium minimum*	**Kalophrynus interlineatus** (Blyth, 1855)
80	*Megophrys monticola*	**Xenophrys** sp
81	*Megophrys monticola nasuta*	*Megophrys nasuta* (Schlegel, 1837)
82	*Megophrys carinensis* [sic]	**Brachytarsophrys carinensis** (Boulenger, 1889)
83	*Megophrys feae*	**Brachytarsophrys feae** (Boulenger, 1887)
84	*Megophrys longipes*	**Xenophrys** sp
85	*Megophrys parva*	**Xenophrys** sp
86	*Megophrys aceras*	*Xenophrys aceras* (Boulenger, 1899)
87	*Megophrys major*	*Xenophrys major* (Boulenger, 1908)
89	*Hyla annectens* [sic]	**Rana (Odorrana) andersoni** Boulenger, 1882
90	*Occidozyga lima*	*Occidozyga lima* (Gravenhorst, 1829)
91	*Phrynoglossus magnapustulosus*	**Limnonectes** sp
92	*Phrynoglossus martensi*	**Phrynoglossus** sp
97	*Phrynoglossus laevis*	**Phrynoglossus** sp
98	*Staurois larutensis*	*Amolops (Amo) larutensis* (Boulenger, 1899)
99	*Staurois afghanus*	**Rhacophorus** *feae* Boulenger, 1893
100	*Elachyglossa gyldenstolpei*	*Limnonectes laticeps* (Boulenger, 1882)
101	*Rana leptoglossa*	**Rana (Sylvirana)** sp
102	*Rana tasanae*	**Limnonectes** sp
103	*Rana tenasserimensis*	**Rana (Hylarana) erythraea** (Schlegel, 1837)
104	*Rana andersoni*	**Rana (Pelophylax) lateralis** Boulenger, 1920
105	*Rana blythi*	*Limnonectes blythi* (Boulenger, 1920)
106	*Rana macrodon*	**Limnonectes kuhlii** (Tschudi, 1838)
107	*Rana cyanophlyctis*	**Limnonectes** sp
108	*Rana tigerina*	**Hoplobatrachus chinensis** (Osbeck, 1765)
111	*Rana rugulosa*	**Hoplobatrachus chinensis** (Osbeck, 1765)
112	*Rana limnocharis*	**Fejervarya limnocharis** (Gravenhorst, 1829)
113	*Rana erythraea*	**Rana (Hylarana) erythraea** (Schlegel, 1837)
114	*Rana macrodactyla*	**Rana (Hylarana) macrodactyla** (Günther, 1859)
115	*Rana cubitalis*	**Limnonectes** sp
116	*Rana mopus*	**Rana (Sylvirana) cubitalis** (Smith, 1917)
117	*Rana glandulosa*	**Rana (Pulchrana) glandulosa** Boulenger, 1882
118	*Rana chalconota*	**Rana (Chalcorana) chalconota** (Schlegel, 1837)
119	*Rana nigrovittata*	**Rana (Sylvirana) nigrovittata** (Blyth, 1855)
120	*Rana lateralis*	**Limnonectes** sp
123	*Rana hosii*	Same individual as p. 118 as *Rana chalconota*, i.e.
		Rana (Chalcorana) chalconota (Schlegel, 1837)
124	*Rana livida*	*Rana (Hylarana) livida* (Blyth, 1855)
125	*Rana scutigera*	**Rana (Sylvirana)** sp
126	*Rana doriae*	**Limnonectes blythi** (Boulenger, 1920)
127	*Rana kochangae* [sic]	**Rana (Pulchrana) glandulosa** Boulenger, 1882
129	*Rana pileata*	**Limnonectes gyldenstolpei** (Anderson, 1916)

Table 1. (continued).

Page	Name in NUTHPUND (2001)	Corrected name
130	*Rana hacheana* [sic]	*Taylorana hascheana* (Stoliczka, 1870)
130	*Rana laticeps*	*Philautus* sp
135	*Rana cancrivora*	*Fejervarya cancrivora* (Gravenhorst, 1829)
136-137	*Rana fasciculospina* [sic]	*Paa* (*Quasipaa*) *fasciculispina* (Inger, 1970)
139	*Rhacophorus leucomystax leucomystax*	*Polypedates leucomystax* (Gravenhorst, 1829)
140	*Rhacophorus leucomystax sexvogatus*	*Polypedates leucomystax* (Gravenhorst, 1829)
141	*Rhacophorus robinsoni*	*Rhacophorus robinsoni* Boulenger, 1903
143	*Rhacophorus colleti*	*Polypedates* sp
147	*Rhacophorus nigropalmatus*	*Rhacophorus nigropalmatus* Boulenger, 1895
149	*Rhacophorus* (new sp)	*Rhacophorus bipunctatus* Ahl, 1927
153	*Philautus vittatus*	*Polypedates* sp
154	*Philautus hansenae*	*Hyla annectans* (Jerdon, 1870)
155	*Philautus doriae*	*Philautus* sp
156	*Philautus nongkhorensis*	*Philautus* sp
157	*Philautus bimaculatus*	*Polypedates* sp.
158	*Philautus parvulus*	*Polypedates* sp
159	*Kaloula pulchra*	*Kaloula pulchra* Gray, 183.
161	*Kaloula mediolineata*	*Kaloula mediolineata* Smith, 1917
162	*Kaloula baleata*	*Kaloula baleata* (Müller, 1836)
163	*Kaloula aureata*	*Kaloula macrocephala* Bourret, 1942
164-65	*Calluella guttulata*	*Calluella guttulata* (Blyth, 1855)
166	*Glyphoglossus molossus*	*Glyphoglossus molossus* Gunther, 1868
167	*Kalophrynus pleurostigma*	*Kalophrynus pleurostigma* Tschudi, 1838
169	*Microhyla pulchra*	*Microhyla pulchra* (Hallowell, 1860)
170	*Microhyla annamensis*	*Microhyla berdmorei* (Blyth, 1856)
171	*Microhyla ornata*	*Microhyla heymonsi* Vogt, 1911
174	*Microhyla inornata inornata*	*Microhyla ornata* (Duméril & Bibron, 1841)
175	*Microhyla inornata lineata*	*Microhyla inornata* (Boulenger, 1890)
176	*Microhyla berdmorei*	*Microhyla butleri* Boulenger, 1900
177	*Microhyla heymonsi*	*Microhyla heymonsi* Vogt, 1911

The error rate of taxonomic allocation is very high in this book, out of 81 species photographed, only 36 are allocated to the proper species. The taxonomy corresponds to the level of TAYLOR (1962) and no recent results, even the most conservative, have been introduced. In conclusion this book should not been considered as a reference for any scientific work.

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Recent books on the amphibians of Europe

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Birgit GOLLMANN & Günter GOLLMANN. – *Die Gelbbauchunke: von der Suhle zur Radspur*, Bielefeld, Laurenti Verlag, *Beiheft der Zeitschrift für Feldherpetologie*, **4**, 2002: 1-135, 35 figures and 4 tables. Softbound. ISBN 3-933066-10-7.
Andrea AMBROGIO & Luca GILLI – *Il tritone alpestre. Tassonimia. Distribuzione. Sviluppo. Ecologia. Etologia. Protezione*. Cavriago, Planorbis, 1998: 1-64. Softbound.

In the series of monographies on European amphibians, a book on the yellow-bellied toad, *Bombina variegata* (Linnaeus, 1758) was missing. This species seems to be particularly endangered and many populations have disappeared in the last decades. A summary of our knowledge on these toads should be an important aid for conservation biologists and environmentalists.

The book by Birgit & Günter GOLLMANN is written in German language. It is original in adding to the known data from the literature many new and unpublished observations. The review is clearly documented by references and accompanied by many figures. Specimens and habitats are presented in colour photos.

The phylogeny, taxonomy and systematics are reviewed shortly. Data on size variation and colour variation try to describe the large differentiation between populations and subspecies, whose phylogenetic relationships have been investigated by various methods. The phenomenon of hybridization with the sister taxon *Bombina bombina* (Linnaeus, 1761) is shortly presented.

Habitat of the species includes breeding places, hibernation and aestivation areas. *B. variegata* shows a large scale of breeding environments which include secondary habitats as road ditches and lairs, but many other kinds of small water bodies. Not much is known on aestivation and hibernation places.

Yellow-bellied toads are then presented as predators and victims, giving lists of prey and predators but also treating the behaviour of the toads. A nice description tries to elucidate form and function of the "Unkenreflex". *B. variegata* shows annual and diurnal activity cycles, in particular in the presence of different life stages in the habitat, and in relation to reproduction. In most anurans the bulk of data available concerns reproduction: place and date, regulation, mating call – or advertisement call as it should better be named –, amplexus, egg laying. It is particularly difficult to obtain simple data like clutch size in these toads, as they lay eggs in several patches. Observations of multiple breeding were made both in males and females. Embryonic and larval development are described, providing data on morphology, nutrition, influence of temperature and density, as well as results from competition experiments. Finally various aspects of metamorphosis are discussed to conclude the description of the life cycle.

An interesting part of the book presents the spatial distribution of the toads. Based on observations of individual toads – recognised thanks to the particular ventral pattern which is unique and remains rather constant throughout the life of a toad –, observations of migration, choice of mating places, immigration in new habitats, periods spent on breeding ponds and fidelity to a certain place are given. This raises the question of spatial orientation on which no recent investigations have been made.

Another question concerns longevity, and we learn that individuals of more than 15 years have been observed in the wild, and that these toads may reach 29 years in captivity. Sexual and age composition of toad populations are presented and variations between the populations are discussed. Population dynamics of different life history stages show major differences, the early stages being particularly affected by loss.

A chapter on conservation discusses legal situations of protection of the toads, and causes of threats. The use of land by man leading to the loss of wetlands is mentioned as a major factor. Isolation of suitable habitats, introduction of fish and also pollution might be factors for regression of this species. The authors claim actions for habitat protection and management in order to protect the yellow-bellied toad. Introduction of alien specimens in populations should be avoided because it leads to genetic pollution.

In a final chapter, the methodology of study is presented in order to encourage the reader to study these interesting animals. This is a basic book, interesting for the herpetologist and the conservationist, who look for precise data on *Bombina variegata*, and in particular for the student, as it stimulates observation and study of these nice and secretive animals.

.*.

Andrea AMBROGIO and Luca GILLI published a nice booklet on the Alpine newt, *Triturus alpestris* (Laurenti, 1768). It is well done, pleasantly presented book, reflecting the famous Italian sense of taste. Color photos and figures are of high quality. The pencil sketches recall the notebook of a naturalist. All details of the book are thoroughly drawn, like the small figures on right top of the right pages that illustrates ontogenetical development of the newt.

The authors present the species by an introduction to its taxonomy and systematics, giving description of external morphology of the Italian subspecies. Then the geographical and altitudinal distributions of these subspecies are shown and discussed. The chapter on the habitat is documented by numerous photos representing as well the ponds and landscapes as the underwater biotopes where the newts live.

In a large chapter on eco-ethology, the feeding behavior of adults and larvae is presented in its different aspects, such as annual variation, nutrition in water and on land, nutrition of adults and larvae, composition of diet, but also predation of newts. Another aspect shown is the life history and population structure of Alpine newts. This chapter is completed by the presentation of the amphibian species syntopic with this newt and their daily activity patterns.

The reproduction of *Triturus alpestris* is introduced in a well-documented part. Many color photos illustrate the descriptions of the breeding behavior showing the male-female interactions. The whole sequence is then summarized and presented in color drawings. A figure explaining the particular terms of the behavior shows small sketches of the movements and their names. The chapter finishes with the description of the egg-laying behavior of the female.

Then the book follows the life history of the newt in presenting a chapter on the development, growth and metamorphosis. Beside normal development and its parameters, the particular case of neoteny or pedomorphosis is described. A clear scheme depicts the live cycle of *Triturus alpestris*.

The book finishes on an important aspect, the conservation of the Alpine newt giving the protection status of the Italian populations. The content of the book is thoroughly documented by the relevant literature, so that the reader can find original publications concerning all subjects.

In summary the book is an interesting presentation of this species, in particular for the Italian peninsula. It is written in Italian, but the rich illustrations make it attractive for all herpetologists. It seems to be the first booklet of a series from this editor and a second on the fire-bellied toads of the genus *Bombina* is announced.

ALYTES

International Journal of Batrachology
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SHORT GUIDE FOR AUTHORS
(for more details see *Instructions to Authors*, see *Alytes*, 1997, **14**: 175-200)

Alytes publishes original papers in English, French or Spanish, in any discipline dealing with amphibians. Beside articles and notes reporting results of original research, consideration is given for publication to synthetic review articles, book reviews, comments and replies, and to papers based upon original **high quality illustrations** (such as colour or black and white photographs), showing beautiful or rare species, interesting behaviours, etc.

The title should be followed by the name(s) and address(es) of the author(s). The text should be typewritten or printed double-spaced on one side of the paper. The manuscript should be organized as follows: English abstract, introduction, material and methods, results, discussion, conclusion, French or Spanish abstract, acknowledgments, literature cited, appendix.

Figures and tables should be mentioned in the text as follows: fig. 4 or tab. 4. **Figures should not exceed 16 × 24 cm**, the size of the lettering should ensure its legibility after reduction. The legends of figures and tables should be assembled on a separate sheet. Each figure should be numbered using a pencil.

References in the text are to be written in capital letters (BOURRET, 1942; GRAF & POLLS PELAZ, 1989; INGER et al., 1974). References in the *Literature Cited* section should be presented as follows:

BOURRET, R., 1942. – *Les batraciens de l'Indochine*. Hanoi, Institut Océanographique de l'Indochine: i-x + 1-547, pl. 1-4.

GRAF, J.-D. & POLLS PELAZ, M., 1989. – Evolutionary genetics of the *Rana esculenta* complex. *In:* R. M. DAWLEY & J. P. BOGART (ed.), *Evolution and ecology of unisexual vertebrates*, Albany, The New York State Museum: 289-302.

INGER, R. F., VORIS, H. K. & VORIS, H. H., 1974. – Genetic variation and population ecology of some Southeast Asian frogs of the genera *Bufo* and *Rana*. *Biochem. Genet.*, **12**: 121-145.

Manuscripts should be submitted in **triplicate** either to Alain DUBOIS (address above) if dealing with amphibian morphology, anatomy, systematics, biogeography, evolution, genetics, anomalies or developmental biology, or to Thierry LODÉ (address above) if dealing with amphibian population genetics, ecology, ethology or life history, or to Stephen J. RICHARDS (address above) if dealing with conservation biology, including declining amphibian populations or pathology. Acceptance for publication will be decided by the editors following review by at least two referees.

If possible, after acceptance, a copy of the final manuscript on a floppy disk (3 ½ or 5 ¼) should be sent to the Chief Editor. We welcome the following formats of text processing: (1) preferably, MS Word (1.1 to 6.0, DOS or Windows), WordPerfect (4.1 to 5.1, DOS or Windows) or WordStar (3.3 to 7.0); (2) less preferably, formated DOS (ASCII) or DOS-formated MS Word for the Macintosh (on a 3 ½ high density 1.44 Mo floppy disk only).

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